THE CALIFORNIA ANNUAL GRASSLAND ECOSYSTEM

A Symposium
Sponsored by the California Chapter
American Society of Agronomy
Anaheim, California
January 30, 1975

Edited by

R. Merton Love

Institute of Ecology Publication No. 7

THE CALIFORNIA ANNUAL GRASSLAND ECOSYSTEM

TABLE OF CONTENTS

PREFACE TO THE SECOND PRINTING

The occasion of the second printing of this volume affords two opportunities. One is to designate this collection formally as Institute of Ecology Publication No. 7, and thereby to recognize the valuable service performed by its Editor, while he was Acting Director of the Institute, in bringing some semblance to order to what had previously been a mess. The Institute had never had a publication series worthy of the name and it is to Merton Love's credit that he corrected this situation. He not only sorted and numbered those publications that did exist, he also saw to it that additional publications were issued and the basis for a continuing series of publications established. Such small services to the community of scholarship too often go unrecognized.

The second opportunity is that of noting the recent changes in the publishing program of the Institute. To the series of publications that emanated from interest in the ecology of California's brushlands and wildlands, there has now been added a volume on ecology and conservation of vernal pools and the first item in a new series to be published jointly with the Institute of Governmental Affairs. A complete list of publications is appended to this volume.

The Institute will continue to publish research results that reflect the varied interests of its associated faculty and students, work that underlines the links the Institute enjoys with other organized research units, and analysis that would not ordinarily appear in scholarly journals either because of its length or its unconventional form.

The Institute has a responsibility to give University scholars some priority in its publishing endeavors. There is, however, no compelling reason to exclude important contributions from other authors. Those who have potential contributions to submit for consideration are encouraged to do so.

G. A. Wandesforde-Smith
Acting Director

November, 1976

[illegible] TO THE SECOND PRINTING

[illegible] this volume affords the oppor- [illegible] formerly as Institute of [illegible] to recognize the valuable service [illegible] Director of the Institute, [illegible] has continually been a demand. [illegible]

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FOREWORD

This is the third symposium dealing with California's renewable natural resources sponsored by the California Chapter, American Society of Agronomy. The first, held in Sacramento in January, 1973: "Maintaining the Environmental Quality of California Wildlands" included discussions of the problems, responsibilities, and solutions proposed by the Bureau of Land Management, the National Park Service, the United States Forest Service, and the Pacific Gas and Electric Company. It concluded with the statement on the role of fire in maintaining wilderness quality.

The second symposium, held in Fresno in January, 1974: "Resources for the Future" focused on the importance of these wildlands for future generations, with emphasis on the brushlands and rangelands, and a look at natural resources management of our military installations. It concluded with a discussion of the interrelations of fish, wildlife, people, and agriculture, four factors that have been the essence of life and living since man appeared on the scene.

This symposium concentrates on the annual grassland ecosystem, the mainstay of California's beef and sheep industry, the annual income of which is currently valued at about one and a half billion dollars. Outdoor recreation, too, owes a lot to the grassland ecosystem, probably contributing more than 10 million dollars annually to the state's revenues from fish and wildlife stamps, tags, and licenses, alone.

This symposium is a preview to a publication to be called "Structure, Function, and Utilization of the Annual Grassland Ecosystem", one of a series of seven grassland ecosystems within the Grassland Biome, all of which will be published in the near future.

The California Chapter, ASA, is grateful to the grassland researchers for the time and effort they contributed to this symposium, and I take this means of thanking them personally.

R. Merton Love
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This is the third symposium dealing with California's renewable natural resources sponsored by the California Chapter, American Society of Agronomy. The first, held in Sacramento in January 1972, "Maintaining the Environmental Quality of California's Grasslands" included discussions of the problems, responsibilities, and activities sponsored by the Bureau of Land Management, the National Park Service, the United States Forest Service, and the Pacific Gas and Electric Company. It concluded with the statement on the role of fire in maintaining rangeland quality.

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This symposium concerns one of the state's grassland ecosystems, the wellbeing of California's livestock industry, the annual income of which is currently valued at about one and a half billion dollars. Outdoor recreation, [illegible] the grassland ecosystem, probably contributing more than 50 million dollars annually to the State's revenues from fish and wildlife licenses, tags, and fishing licenses.

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R. Merton Love
Editor

CHAPTER I

AN OVERVIEW OF THE ANNUAL GRASSLAND ECOSYSTEM SYNTHESIS EFFORT

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The International Biological Program (IBP) was established in the 1960's in several countries throughout the world to examine the biological basis of productivity in human welfare. The implications of the objectives were that mankind faced food, fiber, and energy shortages and thus must learn to use natural resources in a way that would not disrupt the resource base itself.

To implement the objectives of the IBP the United States established studies to analyze the structures and functions within ecosystems in six Biomes. Structure refers to the parts of the ecosystem that can be measured in units of energy or mass per unit area. Function refers to the roles that structural components play in an ecosystem, with emphasis on system interactions. Biome is defined loosely as a generalized vegetational form which includes its associated animals and microorganisms. The six biomes represented in the United States are the Grasslands, Tundra, Desert, Eastern Deciduous Forest, Coniferous Forest, and Tropical (Fig. 1).

Charged with responsibilities within the Grassland Biome is a group headquartered at the Natural Resource Ecology Laboratory at Colorado State University in Fort Collins. The task of this central group is to coordinate and help integrate analysis of information efforts in various grasslands in the western United States. Grasslands ecosystems receiving primary emphasis are the tallgrass prairie, mixed-grass prairie, shortgrass prairie, desert grassland, mountain grassland, shrub-steppe grassland, and annual grasslands (Fig. 2). The annual grassland was represented by the site at the San Joaquin Experimental Range, U. S. Forest Service, near Fresno, California.

In 1968 the Grassland Biome began a multidisciplinary and (fortunately) interdisciplinary effort to collect uniform types of information about energy flow and nutrient cycling in the seven different grassland ecosystems. The grassland ecosystem are described in terms of abiotic, producer, consumer, and decomposer components. The concept of multidisciplinary studies means that scientists with backgrounds not only in the classical biological and agricultural sciences but also in mathematics, computer science, statistics, engineering, meteorology, etc., were mobilized to attack (using the systems approach) the extremely complex puzzle of interactions of ecosystems components. The concept of interdisciplinary implies that these scientists will work together.

The systems approach entails: 1) compiling, condensing, and synthesizing information on the components of the system; 2) examining in detail the structure of the system; 3) translating this knowledge of systems components, function, and structure into models (conceptual and mathematical) of the system; and 4) using the models to derive new insights about the management and utilization of grassland ecosystems. The arsenal of tools used to gain this new insight includes detailed examination of the literature, field and laboratory studies, conceptual, statistical, and mathematical models, and, most important, the experience and understanding of knowledgeable field scientists.

The means chosen to convey to the public-at-large information about each of the seven grassland ecosystems within the Grassland Biome network is through the development of comprehensive individual treatments in the form of "type volumes" or users manuals. These volumes will be "state-of-the-art" reference manuals with special emphasis on "stage-of-the-ignorance." The objective of this synthesis effort is to present information that is pertinent and relevant about ecosystems and to define what is not known and should be studied in light of our nation's new emphasis on increased utilization of grasslands.

The synthesis effort of specific interest in California will produce a volume called "STRUCTURE, FUNCTION AND UTILIZATION OF THE ANNUAL GRASSLAND ECOSYSTEM," with a completion date anticipated in 1976. This volume will emphasize processes and controls of processes operating on and in the ecosystem. Understanding such processes requires a thorough knowledge of ecosystem history and structure. Thus, the interdisciplinary-interagency approach of this project is to identify relevant information and evaluate the data in terms of the entire ecosystem. Much of the information and past research efforts on annual grasslands has had limited circulation because it occupies a relatively small geographical area and has minimal professional interest. The broad base of expertise devoted to this synthesis effort includes scientists from the Agricultural Research Service, Reno, Nevada; California Division of Forestry; California State University, Fresno; Naval Post Graduate School; Bureau of Sports, Fisheries, and Wildlife; University of California at Berkeley and Davis; U. S. Forest Service at Fresno; and Colorado State University.

The relationship of scientific journal articles and individual projects to a comprehensive synthesis is important. The synthesis volume does not have as its main intent the reporting of original results except where unpublished material must be used to fill gaps of information. That is, the synthesis volume is not to replace papers for scientific journals. The synthesis volume will tend to cross individual projects and compare ecosystems components rather than to elaborate detailed findings within individual projects.

The volume has several characteristics and purposes:

* It is to be an integrated synthesis of information rather than a collection of individual isolated articles.

* It will relate IBP data sets collected at the San Joaquin Experimental Range to specific information from non-IBP sites.

* It is to include information from experimental projects in the field and laboratory as well as conceptual and simulation modeling studies.

* It will use as example sites the San Joaquin Experimental Range, Hopland Field Station, and Sierra Foothills Research Station.

* As a single source (reference manual) it is anticipated to reduce the need for extensive data searches, which are now being duplicated by researchers, planners, political decision makers, environmental groups, state and federal agencies, etc. It should also reconcile conflicting views due to varied data sources and interpretation.

Output from this project can provide direction to future grassland research and educational programs. The modeling exercises will identify the components that have the greatest influence on the ecosystem. In developing these models, assumptions will have to be made to arrive at specific results. Testing these assumptions will often require further research or long-term observations.

The synthesis effort should also provide insight as to needed areas of emphasis to strengthen our understanding of the functioning of this ecosystem. Information can be reconstituted for a variety of audiences for educational purposes in schools or for special-interest groups so as to

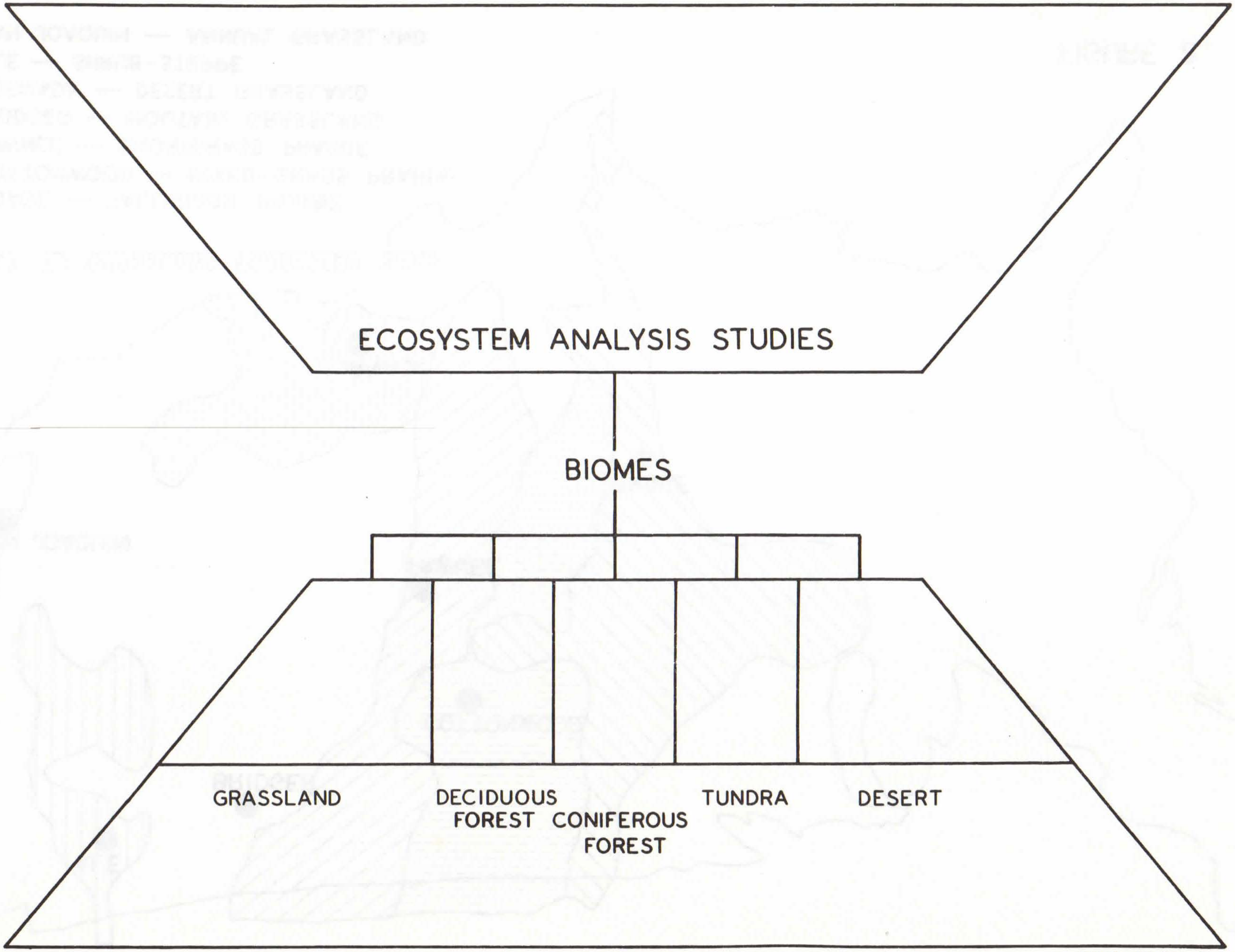
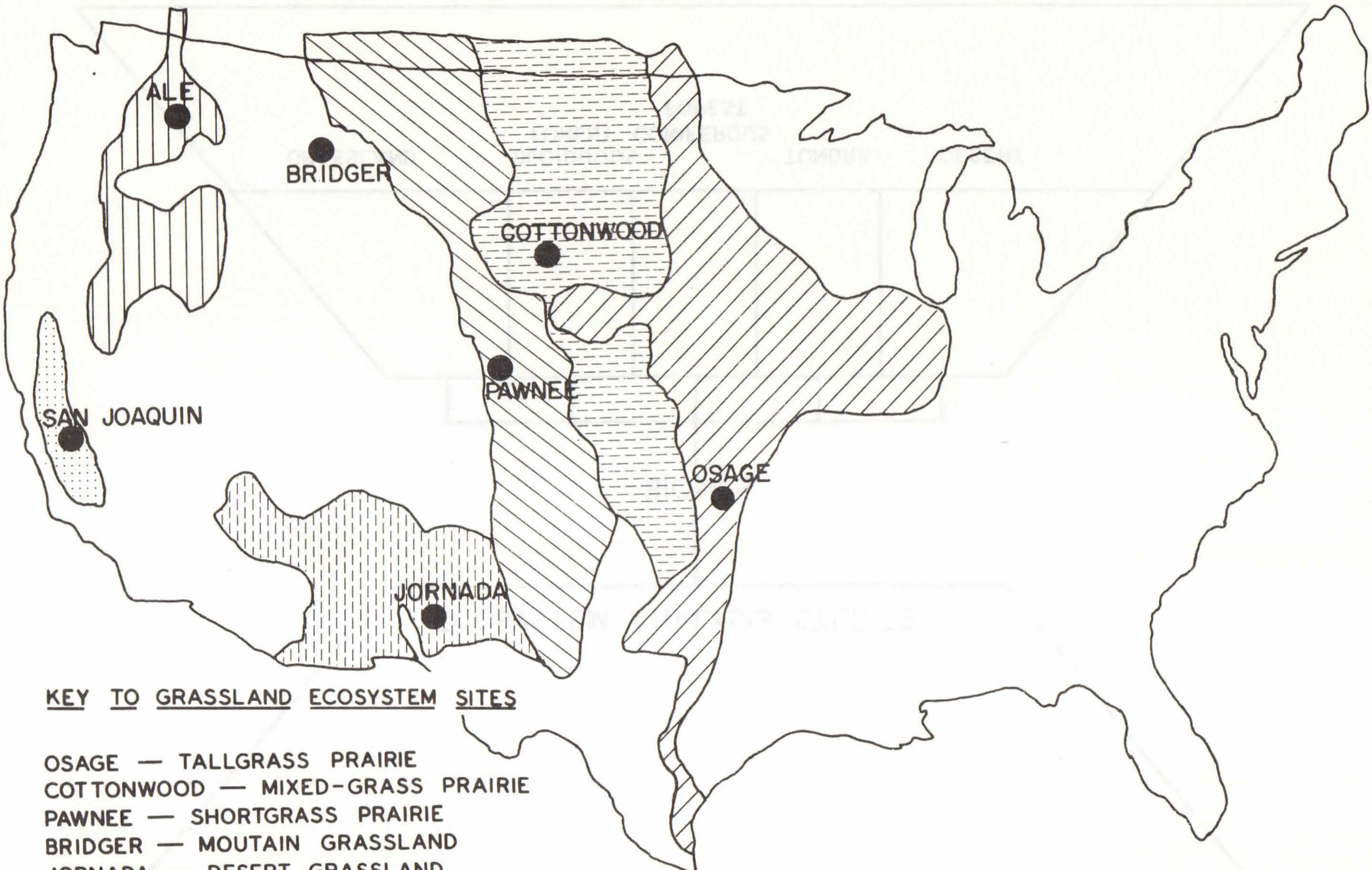

ECOSYSTEM ANALYSIS STUDIES
BIOMES
GRASSLAND
DECIDUOUS FOREST
CONIFEROUS FOREST
TUNDRA
DESERT

FIGURE I.



KEY TO GRASSLAND ECOSYSTEM SITES

OSAGE — TALLGRASS PRAIRIE
COTTONWOOD — MIXED-GRASS PRAIRIE
PAWNEE — SHORTGRASS PRAIRIE
BRIDGER — MOUTAIN GRASSLAND
JORNADA — DESERT GRASSLAND
ALE — SHRUB-STEPPE
SAN JOAQUIN — ANNUAL GRASSLAND

FIGURE 2.

provide a better understanding of the entire system as well as individual components.

Providing this information to users will be a major accomplishment, it can be used in training programs for public-agency personnel, where the situation is common that people trained in natural-resource management are not familiar with the annual grasslands, because of education and experience in other geographic areas. This project can provide important references and data for improved understanding by staff who do not have the benefit of the knowledge of this complex system and are faced with decisions and judgement values. This project can be used to provide all with a most comprehensive look at important natural resources.

Land use decisions are now made upon consideration of two few of the ecosystem components. This is true whether dealing with a political decision or a ranch operation. Economic, social, or environmental impacts can be determined in a more systematic manner with improved understanding of the system. Thus, this effort should prove valuable to private and public resource managers.

The following papers provide a more complete view of this synthesis effort. Dr. Don Duncan will discuss the specific IBP-Annual Grassland Ecosystem site at the San Joaquin Experimental Range in Madera County and the type of information being generated. The climatic, structural, and historical features of this ecosystem will be presented by Dr. L. T. Burcham. Abiotic and autotrophic components of the ecosystem are put into perspective by Dr. John Menke. Down the line, Dr. Frank Schitovsky covers the heterotrophic components: herbivores, carnivores, and decomposers. Special use problems and the potential of the ecosystem are identified by Dr. C. A. Raguse. "Putting it all together", through the use of simulation modeling, will be approached by Dr. W. A. Williams. Through these efforts, our understanding of the annual grassland ecosystem will improve and lead to more satisfactory decisions on resource use.

CHAPTER II

THE SAN JOAQUIN SITE OF THE GRASSLAND BIOME:
ITS RELATION TO ANNUAL GRASSLAND ECOSYSTEM SYNTHESIS

BY

Don A. Duncan, Research Ecologist
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Berkeley, California stationed at Fresno, California

The Annual Grassland Site of the Grassland Biome, US/IBP, was established at the U. S. Forest Service's San Joaquin Experimental Range in 1972. The Experimental Range is representative of lower-foothill annual grasslands in the granitic soil area of central California. The 4,500-acre Experimental Range is in Madera County in the lower Sierra Nevada foothills at elevations varying from 700 to 1700 feet. The area is in the annual plant-oak woodland type. The Grassland Biome site is in an open, grassland area. The soils on the Site (Ahwahnee series) are relatively shallow, with a low water-storage capacity. The area has mild, moist winters and hot, dry summers. Annual precipitation for the last 40 years has averaged about 19 inches, with extremes of 10 and 32 inches.

The annual vegetation [the more important components are several species of brome (Bromus spp.), fescues (Festuca spp.), filaree (Erodium spp.), and clover (Trifolium spp.)] germinates with the first good rain in the fall. The plants grow slowly during the winter months, then rapidly in the early spring until soil water becomes limiting, in April, May, or early June. Then the annual plants mature and die. The following paper, by Dr. Lee Burcham, will go into greater detail on the overall makeup of the annual grassland ecosystem.

Information was collected on the San Joaquin Site throughout the 1973 and 1974 seasons on the abiotic, producer, consumer, and decomposer components of the ecosystem, in the same form followed for six other grassland ecosystems. These annual grassland data are in the main in the Grassland Biome data bank at the Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins. Some preliminary results from first-page analyses are highlighted in this paper.

Abiotic

Precipitation was slightly above average at the San Joaquin Site in both the 1973 and 1974 seasons, being 24 inches in 1973 and 23 inches in 1974, compared with the 40-year mean of 19 inches. Temperatures were about normal; for example, in 1973 the average daily maximum for July was 97° F (35-year mean was 98) and the average daily minimum in January was 33° F, the same as the long-term mean.

Gravimetric soil water measurements showed about 10 percent water in mid-April, when the herbage was making rapid growth, with a subsequent rapid decline to two or one percent or less by early summer and into fall. In general, soil water did not differ greatly by depth increments--when it's wet, it's all wet; when it's dry, it's all dry.

Producers

Total aboveground biomass in 1973 rose from a few grams per square meter early in the season to over 100 in March to over 300 in April. It peaked in early May at well over 400 grams (Fig.1). The same general pattern occurred in 1974 when aboveground biomass peaked at an identical 458 grams per meter square on the ungrazed treatment in late April (Fig. 2). These aboveground biomass figures are for live growth at the early sampling dates, a combination of live and recent dead plants at the intermediate dates, and primarily recent dead plants on June or July sampling dates. The September sample dates, particularly 1973, include live summer annuals. In both seasons, our data showed the usual pattern for annual grasslands; that is, the majority of plant growth of the early-maturing annuals occurs in March and April, tailing off rapidly as soil moisture declines. In 1973, litter accumulation peaked the next sampling date after the aboveground biomass topped out. Litter on both grazed and ungrazed areas on May 21, 1973 was a little over 300 grams per square meter.

The aboveground biomass figures just cited are for the early-maturing (spring) annuals. In 1973, we obtained information on later-maturing (summer) annuals that was an eye-opener. Most herbage yield data have historically been for the spring annuals, primarily because the summer annuals have little grazing value for domestic livestock. On the grazed study plots 200 grams per square meter were produced between June and September of 1973 (Fig.1). This was primarily tarweed (Hemizonia spp.). Much of this tarweed growth came when gravimetric soil water was less than one percent! The 1974 results showed much less summer annual production: only about 30 grams per meter square from July through September on the grazed plots (Fig. 2).

The 1973 and 1974 seasons were the first attempts to quantify belowground biomass at the Experimental Range. What is happening underground is not fully understood; certainly belowground biomass does not follow a nice, neat seasonal pattern as does the aboveground. The most consistent thing in the belowground data was that there is always considerably more belowground than aboveground, and that the majority of the belowground material was always in the top ten centimeters of soil. As data on the decomposer component of the ecosystem become available, we hope for a better insight into what goes on under the soil surface.

Consumers/Decomposers

In a later paper, Dr. Frank Schitoskey will cover the heterotrophic components of the annual grassland ecosystem. Dr. Schitoskey and a number of graduate students under his direction have handled the small mammal investigations on the San Joaquin Site. Similarly, Dr. Don Burdick (Dept. of Biology, California State University, Fresno), and his graduate students conducted aboveground invertebrate investigations on the Site during the 1973 and 1974 season. The 1973 data on these aspects of the consumer component of the ecosystem are being processed and should be available soon.

Some very preliminary investigations into the role of nematodes on the San Joaquin Site, in cooperation with Dr. James D. Smolik (Plant Science Dept., South Dakota State University) point toward another possibly large "unknown" in the functioning of the annual grassland ecosystem. There were several million nematodes per square meter, which Dr. Smolik summarized by plant-feeding, predaceous, and saprophagous categories. Most of the plant-feeding nematodes were found where most of the plant roots were found, in the top 20 centimeters of soil.

Dr. Jo Anne Pigg (Dept. of Biology, California State University, Fresno) and her graduate students have been studying decomposition rates and CO_2 evolution on the Site.

Other information on the consumers includes cattle weight responses on the San Joaquin Site. Cows and calves grazing on the study area in 1973 showed weight changes very similar to cattle responses in past years. From March to early May, the lactating cows gained about 3 pounds per day when grazing on the plentiful green forage. At the same time, their calves gained a little over two pounds per day. Cow gains dropped off far more rapidly from May to late June than did calf gains. The cows lost weight from late June to late July, but the calves showed some gains until weaned, in late

July.

In conclusion, information from the San Joaquin Site IBP studies for 3 years, along with a great deal of available abiotic, producer, and consumer data from prior studies at the Experimental Range since 1934 (about 250 references), will be used in adapting grassland models to an ecosystem dominated by annual plants. Similarly incorporated as integral parts of the overall annual grasslands synthesis effort will be data from other established research areas in the annual grassland ecosystem, such as the Hopland Field Station and the Sierra Foothills Range Field Station, which represent different climatic and edaphic conditions as discussed in the following paper.

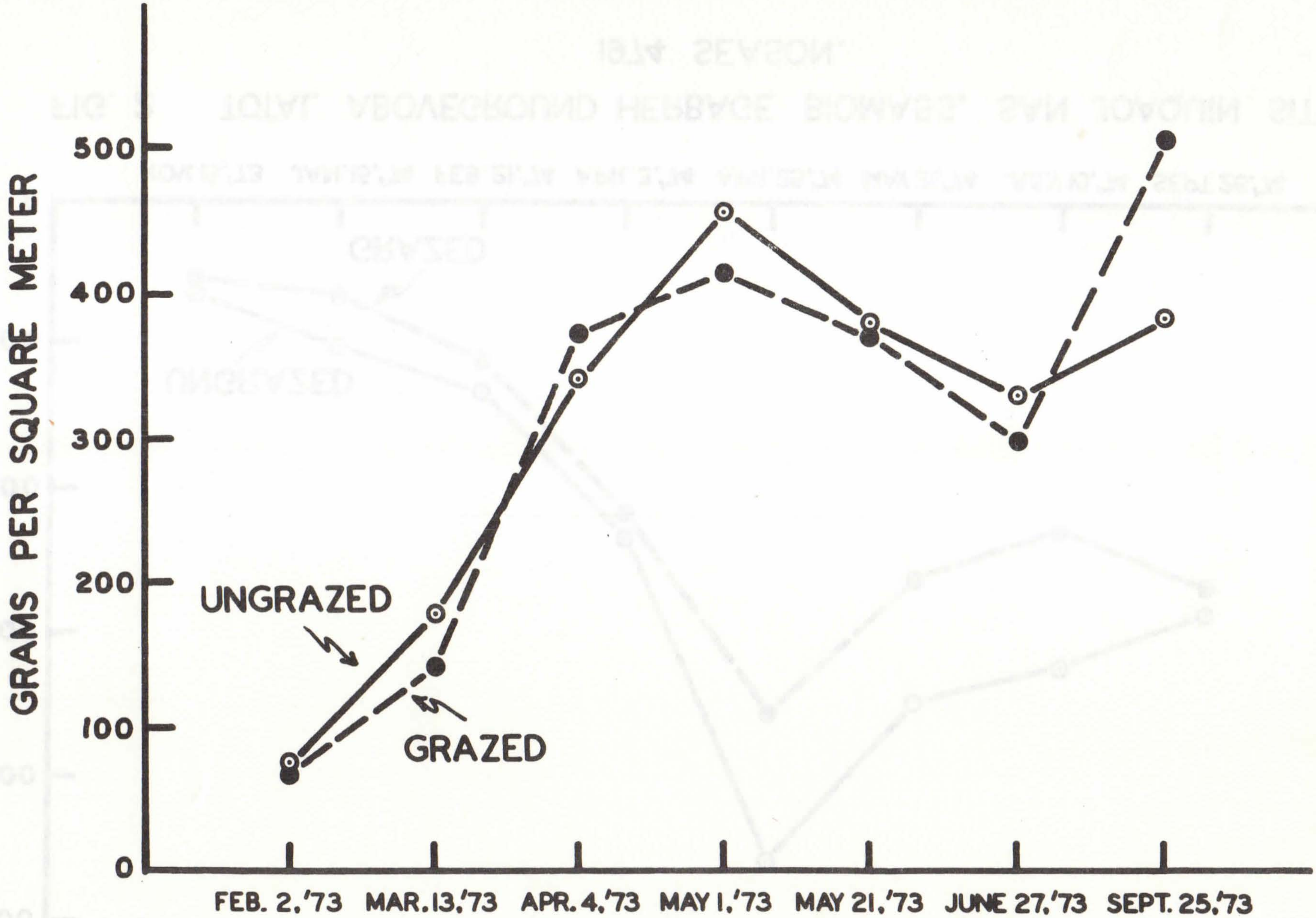

FIG. 1 TOTAL ABOVEGROUND HERBAGE BIOMASS, SAN JOAQUIN SITE, 1973 SEASON.

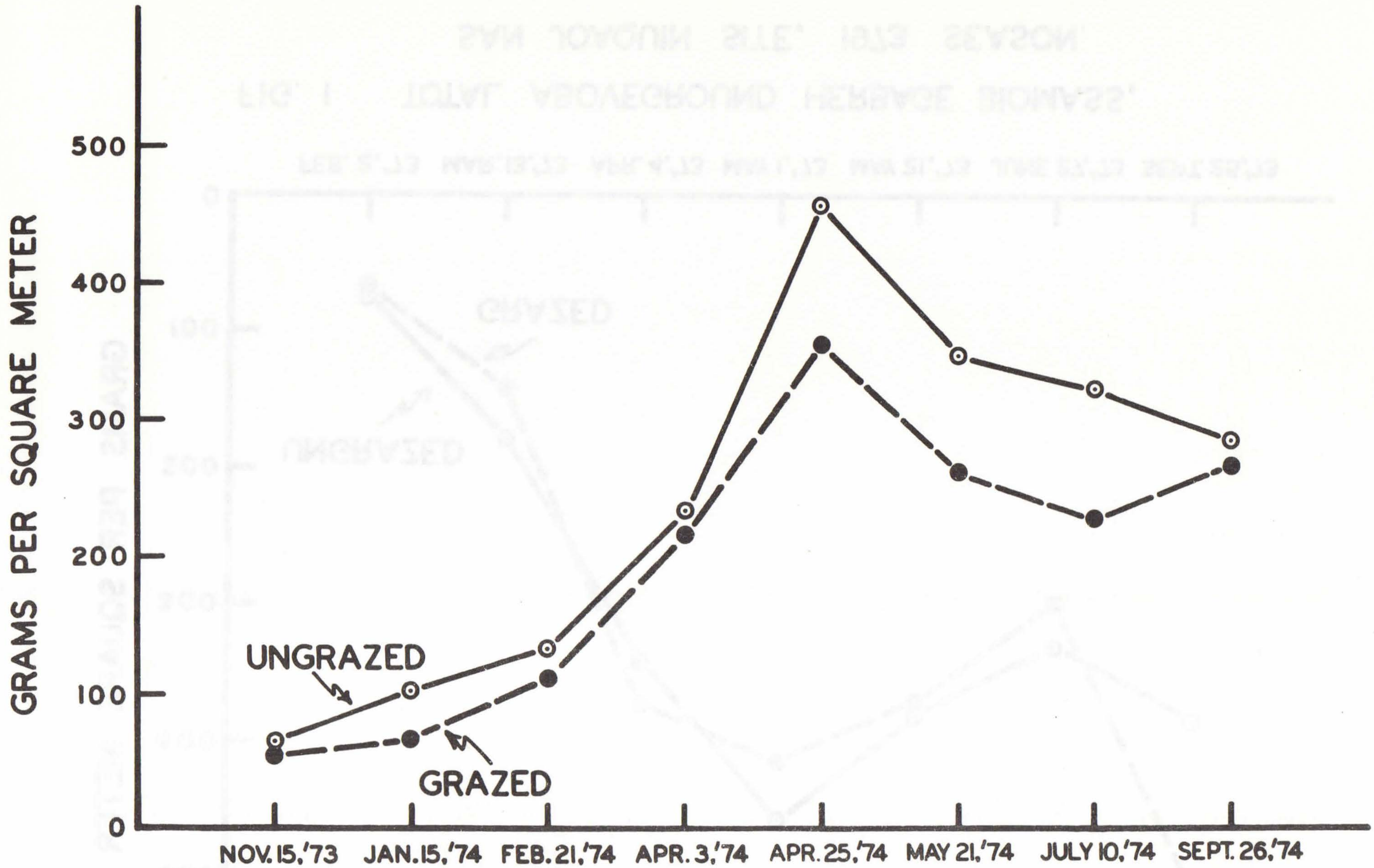

FIG. 2 TOTAL ABOVEGROUND HERBAGE BIOMASS, SAN JOAQUIN SITE, 1974 SEASON.

CHAPTER III

CLIMATE, STRUCTURE, AND HISTORY OF CALIFORNIA'S ANNUAL GRASSLAND ECOSYSTEM

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California Division of Forestry

The California annual grassland ecosystem is a composite, discontinuous plant community embracing open treeless grasslands and continuous and intermingled woodlands. It is constituted of three grassland communities, variously termed valley grassland, coastal prairie, and California prairie; and of three woodland communities, referred to as foothill woodland, northern oak woodland, and southern oak woodland. While geographically extensive and somewhat disjunct, the essential unity of the ecosystem is attested by its distinctive climatic features and physiographic similarity throughout; and by the dominantly herbaceous annual life form of its vegetation, as well as the physiological and phenological responses of the vegetation to factors of the environment.

Geographically, the annual grassland occupies the margins of the Central Valley and the adjacent foothills of both the Sierra Nevada and the Coast Ranges. It includes the low, hot interior valleys--such as Salinas, San Benito, and Antelope valleys--of the South Coast Ranges, together with their surrounding woodlands. It extends southward through the coastal areas from San Luis Obispo County to San Diego. The coastal prairies, scattered grasslands, and intermingled open woodlands of the middle and outer North Coast Ranges, from San Francisco Bay northward into Humboldt and western Trinity counties, are also part of the plant community thus broadly delimited. It extends north and south through about 8 1/2 degrees of latitude, and is some five degrees of longitude from east to west.

Physiographically, the grassland elements of this ecosystem occur on gently undulating open plains and low terraces of the valley floors. They extend upward onto moderately rolling to hilly topography bordering the valleys. They also occupy much of the more level land--swales and stringers--within the woodlands. Woodland portions of the ecosystem are characteristically on more rolling to hilly terrain. In elevation, it lies mainly between sea level and about 3,000 feet, but fingers upward to about 5,000 feet in southern California and on warm slopes in the north.

CLIMATIC TYPES

The Central Valley and its surrounding foothills and the South Coast Ranges have a dry-summer subtropical climate. This climate is characterized by a high percentage of sunshine in all seasons; by dry, warm-to-hot summers; and by mild, rainy winters. Since these conditions prevail also in the regions around the Mediterranean Sea, this kind of climate is often referred to as the Mediterranean, or Mediterranean subtropical, climate. The climatic type known as "Mediterranean" is, in fact, a family of climates, more than one of which occurs in California. About 57 per cent of the state is dominated by this climatic type. Four other regions of the world also have Mediterranean climates.

The middle and outer North Coast Ranges, from San Francisco Bay northward, have a mesothermal marine climate characterized by mild winter, cool summers, and higher rainfall. Its proximity to the ocean and to prevailing on-shore winds make this one of the most equable of climates.

For the annual grassland ecosystem, as for California as a whole, major climatic controls are exerted by latitude, the influence of the Pacific Ocean, and the orientation and extreme range in elevation of the topography, with the last by far the most important (Byers, 1931). Contrary to the usual situation, where latitude is a major determinant of temperature differences, in California the effect of latitude is only minor and is subordinated to that of topography.

Because of its great geographical extent and the significant differences in elevation, there are correspondingly large variations in climatic elements for the grassland ecosystem. Mean maximum temperatures are from 63° to 102° F in summer, and winter minima are from 29° to 45° F. The growing season varies from six months (in the more northerly portions and at higher elevations) to the entire year (in the south). The frost-free period may be as short as 175 days, or as long as 365 days.

Average annual precipitation ranges from 6 inches (in the south) to more than 75 inches (in the northern coastal regions). Practically all precipitation comes during winter, at irregular intervals; it is principally from storm systems generated in the North Pacific Ocean. A major part of it is received as rain, with snow being of limited importance in the inland portions at higher elevation.

An important climatic factor for the vegetation is fog, which is most frequent in coastal and neighboring foothill districts. It increases generally with latitude, and with altitude up to some 2,000 to 3,000 feet. Along coasts and windward slopes it is more frequent in summer than in winter. In winter, fog may be more important in inland areas, including the Central Valley.

Throughout the Central Valley, and in some coastal valleys as well, there are frequently periods of from a few days to more than two months in winter with a temperature inversion under a static or stagnant high-pressure area. At such times, a thick layer of fog forms which may be from less than 500 to as much as 2,000 feet thick. Temperatures then have a narrow diurnal range, sometimes as little as two to four degrees F; there is little wind movement. At these times, a wide band around the edge of the valley is swathed in fog. These winter fogs may occur between late November (after the first significant rains) and early April, but are more prevalent between December and March.

STRUCTURE OF THE VEGETATION

Under the climatic regime prevailing throughout the annual grassland ecosystem, herbaceous plants are dominant. Both grasses and forbs are strongly represented. Grasslike plants (sedges and rushes) are usually present in small numbers, especially in swales and similar more moist areas. These herbaceous annual plants begin growth in fall, the seed germinating after the first "effective rain"--amounting to about one-half inch in a single storm (Bentley and Talbot, 1951). They grow slowly through late winter, the rate of growth depending on weather conditions. The brilliant greens of grasses in the winter season are a vivid contrast to the parched brown landscape of the long, dry summer. The annual vegetation matures by late March or early April in the south; by June in the north. Seed is scattered, and the plants dry up, becoming bleached by the sun and occasional summer rains.

The woodland portion of this ecosystem is a composite community of trees, shrubs, and open grasslands. Trees may be intermixed with shrubs in very open to dense stands, with a total crown cover of woody vegetation ranging from only two or three per cent upward to nearly 100 per cent. In general, tree-herb and tree-shrub-herb subcommunities predominate. Trees are primarily oaks (*Quercus*); Digger pine (*Pinus sabiniana*) is the most common associate; California buckeye (*Aesculus californica*) and others are less frequent. Shrubs are mainly various kinds of *Ceanothus*, *Arctostaphylos*, and Rhamnus. Woody plants of this community tend to be small, with waxy small leaves, mainly evergreen, and often with thick bark. They are usually widely spaced; have very deep or widely spreading root systems; and are adapted in various ways to the long rainless summers.

Throughout the grassland ecosystem herbaceous annual plants are the dominant vegetation life form. They are a strong element even where aspect dominance is maintained by open woodlands, commonly forming essentially a continuous ground cover under all but the densest stands. The original perennial bunchgrass dominants have long been superseded by annual bromegrasses (Bromus), fescues (Festuca), wild oats (Avena), and a long list of others (Burcham, 1957; 1961). Associated with the grasses is a host of forbs, both native and introduced, the most common and widespread being filarees (Erodium); a variety of legumes--bur clovers and true clovers (Medicago and Trifolium), lupines (Lupinus), and trefoils and deervetches (Lotus); and tarweeds (Hemizonia and Madia) and similar late summer annuals.

For the annual grassland ecosystem as a whole the most ubiquitous and abundant plant is soft chess (Bromus mollis). This grass was found in all but one of 38 stands sampled from Sacramento to Madera County in the Sierra foothills and from Santa Clara to Monterey County in the South Coast Ranges (Table 1). In terms of percentage of herbage cover it was the most abundant species in 30 of these stands. Filarees were the second-most important group of plants in terms of both constance and abundance, occurring in 31 of the stands sampled, and being most abundant in 28 of them. Annual fescues, principally Festuca megalura, had a constance value of 50 per cent,

Table 1. Constance and abundance of selected plants in thirty-eight stands of annual grassland.

Species	Constance		Abundance*	
	Number of plots	Per cent of plots	Number of plots	Per cent of plots
Grasses				
Avena	16	42.1	3	7.9
Bromus madritensis	1	2.6	0	
Bromus mollis	37	97.4	30	78.9
Bromus rigidus	21	55.3	1	2.6
Bromus rubens	9	23.7	0	---
Festuca (annual species)	19	50.0	4	10.5
Hordeum	10	26.3	4	10.5
Forbs				
Brodiaea	3	7.9	0	---
Erodium	31	81.6	28	73.7
Hemizonia	7	18.4	2	5.3
Hypocheris	4	10.5	0	---
Lotus	3	7.9	0	---
Medicago	4	10.5	3	7.9

*Based on estimated percentage of forage cover of each species on sample plot.

occurring in 19 of the stands. In abundance, they were equaled by the wild barleys. Ripgutgrass (Bromus rigidus) exceeded the annual fescues in constance but was very low in abundance in these stands.

Native forbs have maintained a much stronger position in the annual grassland flora than have the grasses. Their abundance and variety cause these grasslands to vary markedly in appearance with the progression of the seasons, probably without parallel in any other California plant community. At certain times of the year, from early spring into mid-summer, a given species--or a group of species--may be so conspicuous as to obscure the grasses, creating the illusion of being the dominant vegetation. In this respect, the appearance of these grasslands is frequently reminiscent of descriptions left by early travelers in these regions (Cronise, 1868; Muir, 1911).

The dominance of these seasonal societies and the plants which constitute them vary from year to year, reflecting differences in the amount and seasonal distribution of rainfall, prevailing temperatures, and other weather elements, as well as season of use and intensity of grazing.

DISTINCTIVE FEATURES OF THE CALIFORNIA ANNUAL GRASSLAND ECOSYSTEM

The magnificent forage resource found in California by the early Spanish settlers differed from that of any other range region of North America in a number of ways: in climatic conditions; in composition of the forage cover; and in ecological characteristics and physiological responses of the flora.

The climatic conditions under which the California grasslands developed are distinctive. California grasslands receive their precipitation in winter, essentially all of it as rain. East of the Rocky Mountains, the Great Plains grasslands receive some snow in winter, but their maximum of precipitation is in summer during the growing season. Even the Palouse Prairie of southeastern Washington, which has its major precipitation in winter also, receives some summer rainfall; and year-around temperatures are lower. The distinctiveness of the climate of the California grassland ecosystem is illustrated dramatically when the composite hythergraph for this region is compared with those of the Great Plains grasslands (Smith, 1940), as is done in the model (Fig. 1).

The California prairie--and the grassland elements of contiguous woodlands as well--were distinguished from related floral units of the Pacific Northwest, and from grasslands of the Great Plains by the number and importance of annual plants, and particularly of forbs, in the plant cover (Beetle, 1947). In fact, in some situations annual plants must have been dominant locally. In addition, while many of the genera and some species characteristic of other North American grasslands were represented in the California prairie, most of the dominant species have relatively restricted distributions elsewhere. Finally, the sod-forming grasses, important floristic elements of grasslands east of the Rocky Mountains, were virtually absent from California grasslands.

The fact that California's summer drought is followed by a winter season of comparatively high precipitation has important bearings on the ecological characteristics and physiological responses of the range forage. Plants growing in regions of Mediterranean climate must be adapted to an extremely great range in habitat conditions, especially with respect to heat and moisture, as illustrated in the accompanying model (Fig. 2). They must be able to make appreciable growth during winter, when temperatures are low and soil moisture is at or near saturation levels, with consequent poor soil aeration. In summer, these plants must survive or evade deficiencies of soil moisture, and temperatures comparable with those of the desert.

In California grasslands the period of active growth begins in fall, with the onset of shorter days and lower temperatures. Annuals germinate after the first effective rains, but perennial grasses quite commonly begin growth before fall rains occur (Burcham, 1957; 1961; 1970b). This early growth by perennials depends upon food reserves stored in the root; grazing practices must provide for their replenishment if perennials are to be maintained in the stand. Annuals evade summer drought by maturing seed at the beginning of the dry season; perennials by dormancy. These and related characteristics are major elements in the explanation of what happened to California grasslands under grazing, especially during the first century of use.

GRAZING ON CALIFORNIA GRASSLANDS

Domestic livestock began grazing on California grasslands more than two hundred years ago. The Spanish colonists who founded the first settlement at San Diego in 1769 brought cattle and other livestock with them. Nourished by the excellent forage of the California range lands, the animals thrived, providing many necessities for the new colony. This first settlement was soon followed by others; additional livestock were brought to the province. The livestock industry that developed as settlement progressed constituted the economic foundation of Spanish California until gold was discovered, in 1849. Ranching has continued to maintain its prominence: today it is the most widespread agricultural activity in the state; and for years it has been the foremost agricultural commodity in terms of income produced.

Four phases of ranching can be identified as California progressed from a frontier outpost of New Spain into the Twentieth Century (Burcham, 1961). Development of ranching was accompanied by significant changes in both the area and character of the grazing lands.

Ranches of the Spanish missions dominated the Californian scene from the beginning of settlement until about 1833. Additional missions followed the first one, at San Diego, in rapid succession. By 1823, a chain of 21 missions extended along the coast from San Diego to Sonoma. Ranches of the missions occupied most of the lands in the coastal region held by the Spaniards, about one-sixth of the total area of the state. Probably more than 400,000 cattle and 300,000 sheep grazed on this pastoral empire of the missions (Robinson, 1948). Missions were colonizing agents of the Spanish government, and were not intended to be permanent.

After the mission lands were transferred to the civil government, between 1833 and 1836, liberal grants of land were made to private individuals as an incentive to engage in ranching or agriculture. These Mexican ranchos (Mexico had won her independence from Spain in 1822) succeeded the mission ranches. Operated by private enterprise, they were the centers of ranching activity from the mid-1830's until 1850.

Early American ranches--supplying local demands for animal products, and as speculative ventures--prevailed from about 1850 until the middle 1860's. Discovery of gold in California created an unprecedented market for meat--almost immediately, and literally at the rancher's doorstep. Large quantities of meat were needed in the various mining communities and in the rapidly growing metropolitan centers of San Francisco, Sacramento, and Stockton. A strong demand for meat and an extremely limited local supply of cattle led to major movements of livestock into California from Mexico, Texas, and the Middle West. These conditions also promoted intensive speculation, especially in the cattle industry. Alternating periods of drought and high rainfall in the 1850's and early 1860's wrought havoc with the livestock industry. Hundreds of thousands of animals were drowned in widespread floods in the winter of 1862; and in the next two years possibly a million head died from drought. These drastic consequences of flood and drought permanently curbed cattle ranching on a speculative basis in California. The experiences of that period, however, led to the first positive steps in range improvement and better animal husbandry.

Demands of crop agriculture made the first major inroads upon the open range between 1860 and 1870, which has been characterized as California's "Decade of Wheat" (Wickson, 1923). Great acrages of valley land were diverted from range to wheat production. This period of agriculture and adjustment, from about 1865 until well past 1880, was the fourth phase in the development of livestock ranching. As settlement of the state proceeded and emphasis on farming increased, the era of cheap, free range for livestock was ended in the valleys and certain portions of the foothill country. The pastoral industry shifted to the upper margins of the grasslands and the woodland ranges of the foothills, and to the plateau and mountain portions of the state, where it became essentially stabilized.

CHANGES IN THE GRASSLANDS

Two centuries of grazing and agriculture in California have greatly altered both the extent and character of the grasslands. Approximately 14 million acres of the state are now under cultivation or occupied by urban and industrial areas. The greater part of this area--probably as much as 12 million acres--was originally in the California prairie and woodland plant communities, and hence was predominantly grasslands.

Within the grasslands which remain, the most striking change has undoubtedly been replacement of the native perennial grasses by annual plants, a large proportion of them introduced from the Mediterranean region of the Old World. Few places on earth, if any, have had such a rapid large-scale replacement of native herbaceous vegetation by alien plants. To a large degree it was accomplished within 20 years (between 1845 and 1865), but the process began almost as soon as the first settlement was founded, and it continues even today.

The many crop and garden plants brought to California by early settlers were not of consequence in replacing native vegetation of the grasslands. Plants important in this connection were introduced unintentionally, almost without exception. They came mostly as "hitch-hikers": in packing materials; as impurities in cultivated crops; in ballast; even in the coats of domestic animals. Early accounts confirm widespread distribution of alien plants at a comparatively early date. At least 95 important aliens--mostly annuals--were fairly well established by 1860, with grasses and composites being most numerous (Robbins, 1940).

PLANT SUCCESSION IN THE ANNUAL GRASSLAND ECOSYSTEM

Some of these introduced plants--chiefly grasses--became dominant over great areas of California grassland during rather definite periods, in chronological sequence. Four stages of plant succession which were of major significance in replacing the native perennials by annual plants have been identified (Burcham, 1957); they are illustrated in the accompanying model (Fig. 3). The first stage was characterized by wild oats (Avena) and black mustard (Brassica nigra); it was most prominent between 1845 and 1855. Filarees (Erodium), wild barleys (Hordeum), nitgrass (Gastridium ventricosum), and native annuals represented by foxtail fescue (Festuca megalura) composed the second wave of succession, which was dominant from about 1855 until 1870. Plants such as mouse barley (Hordeum leporinum), red brome (Bromus rubens), silver hairgrass (Aira caryophyllea), Chile tarweed (Madia sativa), and star thistle (Centaurea) were representative of the third stage; it began during the 1870's and is widespread on California grasslands today. A fourth stage, beginning about 1900, is now well established; it is constituted of alien annual grasses--represented by medusa-head (Taeniatherum asperum), barb goatgrass (Aegilops triuncialis), dogtail grass (Cynosurus echinatus), and annual falsebrome (Brachypodium distachyon)--and of forbs such as Hypocheris, Navarretia, Eryngium, and other native and introduced species.

This chronological sequence in dominance of the grassland cover corresponds to the descending scale of annual plant succession. It also indicates a decline in productivity, and reflects intensity of grazing use.

Superficially, the range lands of California did not differ in appearance from many eastern grazing lands. Early ranchers stocked and managed them according to practices with which they were familiar. But the forage cover was deceptively lighter than on grasslands having summer rainfall; production was not renewed through the growing season by abundant rains; and ecological responses of plants of Mediterranean regions to grazing are distinctly different. Disturbances of the plant cover of the grasslands, by grazing and other activities, favored vigorous responses of native annual plants of inferior quality--and of introduced grasses and forbs. Range lands with these characteristics may change strikingly under the impacts of grazing animals.

A major part of the explanation for the changes lies in the adaptations of the plants themselves to the distinctive environmental conditions of Mediterranean lands. These plants evolved in regions having climates similar to California, surviving for centuries on lands grazed heavily by domestic livestock, where all but the most aggressive genetic strains were eliminated (Burcham, 1957; 1970a). They are particularly adapted for distribution by seed. They have a wide range of adaptation to soils and other site factors. They germinate quickly under favorable conditions, grow rapidly, and mature quickly. Great quantities of highly viable seed are produced; a high degree of viability is retained by seed sowed naturally in litter and duff; the same is true of seed stored under only marginally favorable conditions even over a period of years (Burcham, 1957; 1970a). Finally, these plants compete effectively with other species and are able to maintain themselves even in unfavorable situations for periods of many years. These characteristics are held in common by most of our native annuals, as well as by the introduced species.

Largely because of their specialized adaptations and agressive growth, and their tolerance for a wide range of habitat conditions, these alien plants and our native annuals have been able to transform the essential character of our grasslands. The changes in plant composition and vegetation structure have been accompanied by lowered productivity and reduced nutritional efficiency for livestock, resulting in ecologically significant shifts in biotic relationships of the plant-soil-animal complex.

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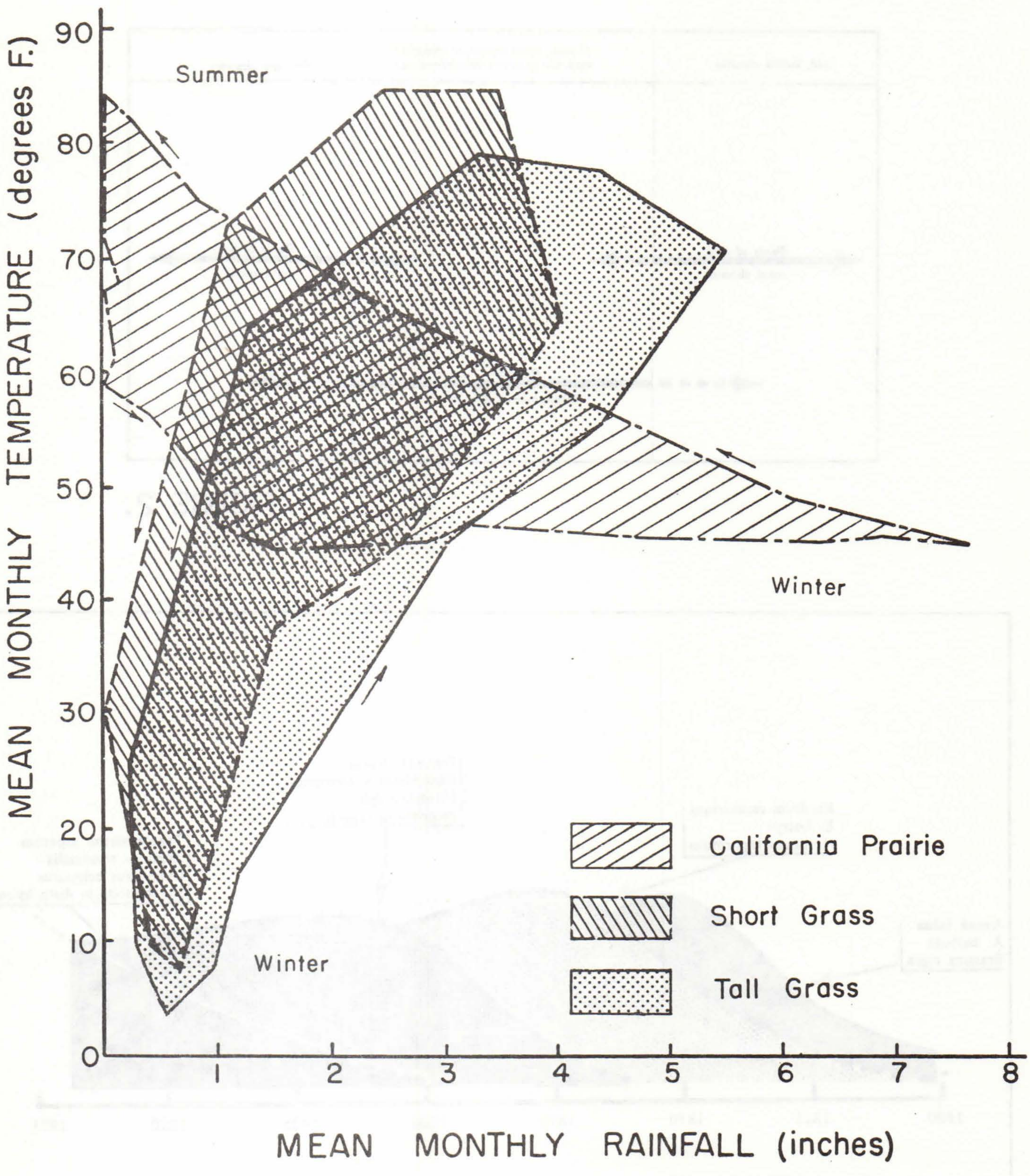
Captions for illustrations.

Fig. 1. The pattern of summer drought and winter rainfall under which the California grassland ecosystem evolved is in great contrast to the summer rainfall and much colder winters of the Great Plains grasslands.

Fig. 2. Plants growing in regions of Mediterranean climate must be adapted to an extremely great range in habitat conditions, especially with respect to heat and moisture.

Fig. 3. Four stages of plant succession which were of major importance in replacing native perennial grasses with annual plants have been identified in California grasslands.



MEAN MONTHLY TEMPERATURE (degrees F.)
90
80
70
60
50
40
30
20
10
0
Summer
Winter
Winter
California Prairie
Short Grass
Tall Grass
1
2
3
4
5
6
7
8
MEAN MONTHLY RAINFALL (inches)

FIGURE 1.

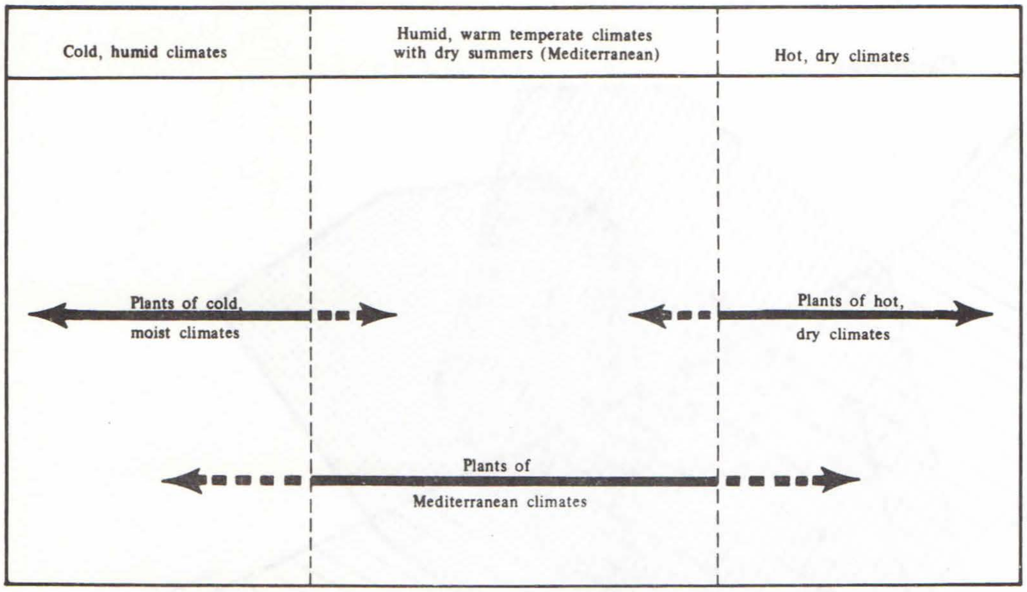


FIGURE 2.

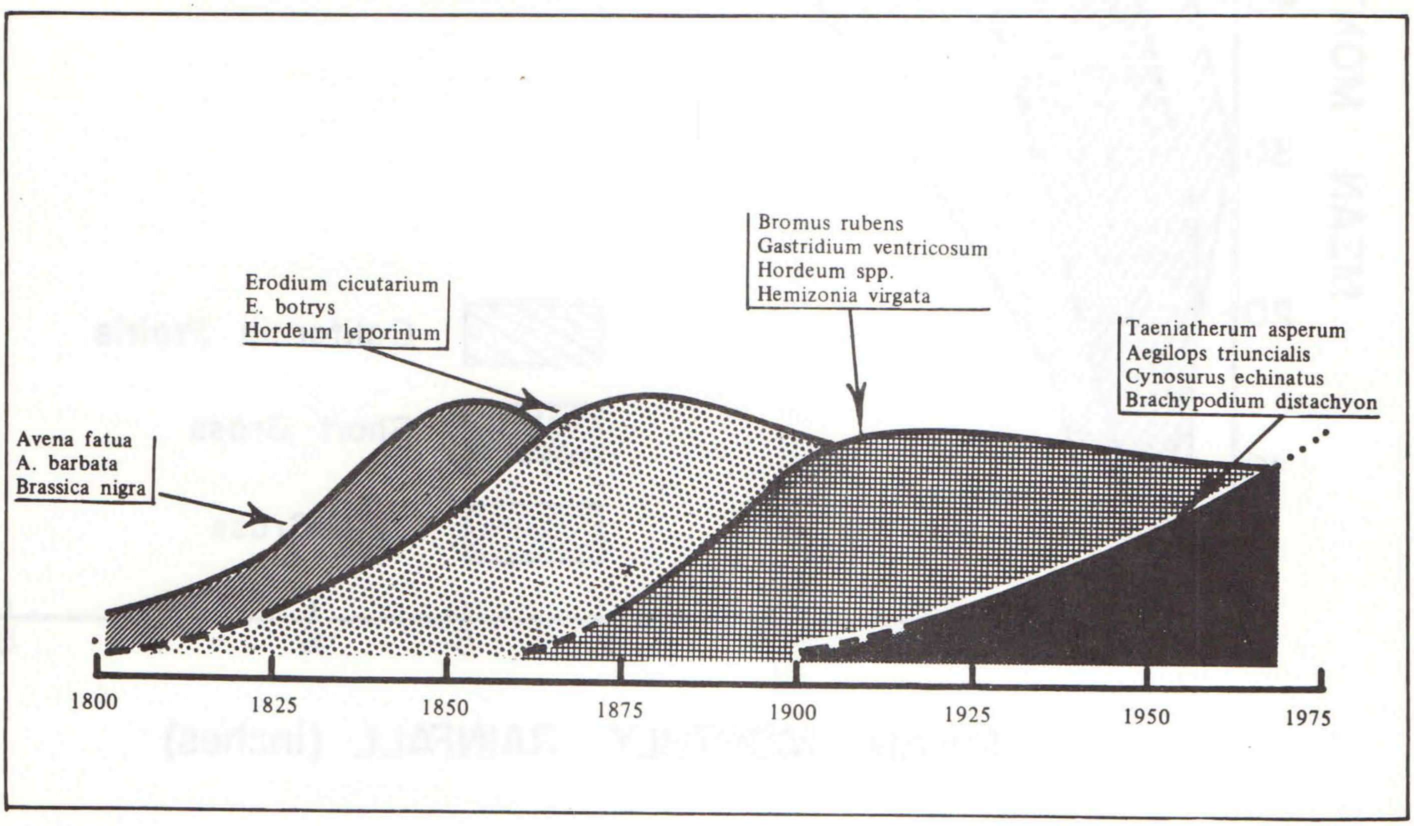


FIGURE 3.

CHAPTER IV

ANNUAL GRASSLAND ECOSYSTEM PROCESSES: ABIOTIC AND AUTOTROPHIC COMPONENTS

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In a systematic approach to analyze ecosystems, it is logical and useful to subdivide knowledge on the subsystems into structural characteristics of the ecosystem components and functional processes through which the ecosystem operates. One might compare this approach with traditional organizations of knowledge by equivalencing broad definitions of anatomy and morphology with ecosystem structure, and equating knowledge in the subject areas of genetics and physiology with ecosystem processes. That procedure is used throughout this analysis of individuals, populations, and communities of organisms under the control and influence of the abiotic components of the ecosystem.

Any treatment and discussion of abiotic processes must at least contain our knowledge on those measurable parameters and biologically significant factors that influence primary productivity and utilization of an ecosystem. For the annual grassland ecosystem these processes include microscale weather, soils, and the interrelationships among microenvironmental factors and biotic responses. Microscale weather is a function of larger mesoscale and, ultimately, macroscale weather patterns, generally termed a Mediterranean type climate for the annual grassland. The driving force for such phenomena is solar radiation.

Insolation can be regarded as the driving force of the ecosystem, and directly related measurable parameters of biological significance: season and diurnal fluctuations in light. In addition, ambient air temperature in the canopy of the plants' leaves and stems has a major role in the growth and development of both annual and perennial grasses and forbs. Seasonal and diurnal changes in air temperature constantly alter rates of photosynthesis and aboveground respiration. One of the major limiting factors in the annual grassland is cool to cold air temperatures during the late fall, winter, and early spring period, which make up the early growth period of many winter-annual species (4,11). Some of our most valuable introduced exotic annual legumes grow extremely slowly during this period, often making their establishment difficult.

Toward the end of a growing season in late spring and early summer and at the potential beginning of a new growing season in early fall, high air temperatures create stress conditions both directly and indirectly by the rapid reduction of soil water through increased transpiration of plants. These conditions, along with strong northerly winds and low relative humidity, can create environments that are extremely desiccating.

Soil temperature at the surface and subsurface of the soil is the second easily monitored parameter resulting from the heat flux from solar radiation. The prelude to primary production or processes of germination and early root and shoot development are under the close control of surface and subsurface soil temperatures, and such factors are critical for an annual grassland community, necessarily starting with these processes each year.

Solar radiation is altered by the standing live plants, litter, or mulch, and by microtopography. The effects of litter or mulch on the annual grassland have been shown to be significant (5,9). In addition to the direct effect of shading plants of lower stature, mulch can buffer the diurnal cycle of surface and subsurface soil temperatures, allowing more favorable conditions for germination and early seedling growth. Mulch has been used in annual grasslands as well as other grasslands as an index to proper utilization. The use of such an index is well founded.

Seasonal and diurnal fluctuations in light and the variability in solar radiation caused by aspect, affecting both light and temperature, result in a complex set of growing conditions. Following the summer drought period and during periods of favorable moisture generally, the level of insolation may be low, and often is, because of cloudy or foggy conditions. Within seasons of rather short day length, especially on north and east exposures, the low level of radiation could definitely affect plant growth and establishment. Temperatures of both air and soil are variables that directly reduce seed germination and seedling growth (11).

Following solar radiation, water is the second major microscale weather parameter influencing primary productivity and fluxes of net primary production. Amounts and patterns of distribution of precipitation are the main values controlling the growth of annual grassland species; yet the relationships among precipitation, total incoming or some measure of effective rainfall, and soil moisture as they affect the growth of different species of annual grassland plants, are not well understood. Forecasts of forage yield have been attempted from precipitation data alone, but with only marginal success (3,8). Interactions between temperature and precipitation appear at this point to be a minimum requirement for any model likely to succeed in predicting annual grassland productivity. One landmark characteristic of this ecosystem is that moisture is limiting when temperatures are conducive to plant growth, and that temperature and often light become limiting when soil water is readily available.

Runoff, infiltration, interception by plants and litter, and storage and depletion of water in horizons of the soil profile have been studied, though usually only in a watershed and vegetation management context. Much additional work in annual grasslands is necessary. Long-term runoff and sedimentation studies have been conducted, with many significant findings (1, 2, 7). In all of those studies, vegetation is related to the runoff cycle through processes of evapotranspiration and interception. In general, replacement of native plant species (with dense canopy, dense and deep roots, remaining in leaf most of the year) by shallow-rooted species with short growing seasons increases water yields as well as watershed forage yields.

Seasonal patterns and amounts of precipitation directly affect the transpiration of plants since shallow annual grassland soils are often depleted of the total available stored soil moisture. Establishment success, growth, competitive ability, and production are all related directly to rates of transpiration. Therefore, abiotic processes affecting transpiration, relative humidity, and secondary factors such as wind, must be considered in the synthesis of microscale weather parameters. Much additional research is needed on the relation of these variables to annual grasslands.

The second major category of abiotic processes is the factor of soil and its direct influence. The processes of prime importance are the parent materials and soil-formation processes that produce a given annual grassland soil of a particular depth, texture, profile development, and nutrient status. Primary production by nonlegumes in annual grasslands is usually limited by nitrogen. The second limiting factor is phosphorus or sulfur. Other nutrients of localized importance are potassium, molybdenum, lime and boron.

Primary production of autotrophic organisms in an annual grassland ecosystem and the subsequent transfer of organic materials is a complex linkage of a host of functional processes under the control of numerous biotic and abiotic factors. One can conveniently categorize the processes into gross primary production, net primary production, and fluxes of net primary production. Taking the breakdown of information one step further, gross primary production is made up of two rather different groupings of processes, one being phenology and the other being the production and partial use of metabolically active carbon compounds. Finally, an example of one process within the second grouping of processes is photosynthesis, which is under the control of soil water, temperature, nutrients, phenology, insolation, photosynthetic pathway, biomass, leaf area, disease, and other factors.

The bulk of our knowledge lies in the area of net primary production or the rates of accumulations in annual grasslands. Probably the strongest link in our understanding of net production in annual grassland ecosystems is the effect of soil nutrient status on herbage production. The independent effects of nitrogen, phosphorus, and sulfur, and the interaction and interrelation of these soil nutrients, are well documented for many grass and legume species.

The major important gaps in knowledge of the system lie in the area of fluxes of net primary production. Rather unknown quantities are the effects of processes such as fire, shoot mortality, root mortality, litterfall, leaching, seed production, and seedling dynamics. Only recently have there been research efforts in a few of these areas. Hopefully, a detailed analysis and synthesis of knowledge concerning abiotic, autotrophic, and heterotrophic processes will redirect efforts into areas of needed research.

Interrelationships among microenvironmental factors and primary producer and consumer responses must be known for a full understanding of the processes affecting the functioning of an ecosystem. For example, the effects of soil nutrients, moisture, and temperature on primary productivity, and the resultant effect of wind, rainfall, and consumers on fluxes of net primary production from standing live or standing dead biomass to litter and mulch, are the first step of a complex of processes. The second step might be that of decomposition of litter and mulch affecting soil organic matter, soil microflora, soil nutrient status, and so on. Processes can conveniently be organized along a nutrient-cycling framework or an energy flow scheme (6, 10).

In annual grassland vegetation, net primary production is partitioned into roots and vegetative shoots during early growth, and into the additional component of fruit development in a later stage before senescence. Some of the seeds carry over to the next growing season. The remainder of the plant structures are disposed of variously: consumed by herbivores, devoured by insects and other microorganisms, decomposed by microorganisms, leached by rains, bleached by the sun, or burned by ground fires. Paralleling these processes in time are shoot mortality, root mortality, and litterfall.

Measurements of seed production show that reproductive structures of the annual-type generally constitute a relatively high proportion of the standing crop. Seed reservoirs on the surface and in the upper layers of the soil are substantial and provide a buffer to various perturbations of the system.

Consumption by domestic herbivores is perhaps the best documented of the processes, and it is well known that the annual type is traditionally utilized intensively and tolerates it quite well. Consumption by wild herbivores is less well documented but is known to assume importance at particular times in cycle with plant phenology. The combined consumption will typically run about 3/4 or more of a standing crop averaging around one ton per acre.

Little attention has been devoted to energy flows to insects and decomposers in the annual type, except for recent research at the San Joaquin Experimental Range. We know from work on other systems that, through litter and root decomposition, raw organic matter is transformed at the autotrophic heterotrophic interfaces into CO_2, mineral decomposition products, and live tissue of the decomposers. An understanding of these processes is extremely important for interpretation of ecosystem behavior because they profoundly affect the nutrient cycle.

Leaching of the dry standing crop by rain has been frequently observed to have the practical consequence of lowering the nutritive value (especially digestible energy) of dry forage. Lysimeter studies of soil leaching show a flush of nutrient movement through the prifle by the first substantial autumn rains, with a strong subsequent tailing-off. Nitrate, sulfate, potassium, calcium, and magnesium are particularly mobile, as in other ecosystems, but the time sequence of transfers under a Mediterranean climate is quite unique.

Fire is seldom used as a management tool in the annual type, but occurs fairly frequently from accidental ignition. Such fire will destroy the standing crop and litter accumulation but is usually a low-temperature fire, only slightly affecting the soil and soil store of seed.

We have but a very sketchy knowledge of energy flows through the annual-type ecosystem since most processes have not been examined in any quantitative detail. We do know that, under a Mediterranean climate, the system has a generally low efficiency in capture of solar energy because of the mismatch between the season of rainfall and the season of high insolation and temperatures favoring plant growth.

Finally, in order to complete a systems-approach treatment of abiotic processes and related autotrophic processes, application of basic information about the annual grassland is related to utilization of the annual grassland ecosystem. In this context, abiotic and autotrophic processes are important as they relate to rangeland utilization and management procedures such as seeding of introduced species, fertilization, grazing, the use of fire, and weed control.

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CHAPTER V

ANNUAL GRASSLAND ECOSYSTEM PROCESSES: HETEROTROPHIC COMPONENTS

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Ecological processes are functions, either biotic or abiotic, that control the flow of energy between the components of an ecosystem (31). Processes involving heterotrophs can be grouped conveniently into six categories: energy flow patterns, food webs, nutrient cycles, diversity patterns, evolution, and controls (23). Energy and nutrients move through the system via food webs. Thus, quantitative studies of food webs yield information on energy flow patterns and nutrient cycles. Since most studies of consumers in the California annual grassland system have dealt with feeding habits, this paper deals primarily with energy flow and food webs.

All heterotrophs can be classified functionally as herbivore, carnivore, or decomposer. Primary producers, plants, provide food for both herbivores and decomposers. Herbivores and decomposers, in turn, provide food for carnivores. Although some decomposers feed on carrion resulting from the death of herbivores and carnivores, the majority of energy entering the decomposer food web is of plant origin. In fact, over 60% of the net primary production in grasslands is consumed by decomposers (18).

Although energy flows through the system, nutrients are cycled in the system. As energy flows through the system, some is lost as heat at each level of the food web. As nutrients cycle through the system, relatively little is lost unless an organism is removed from the system through harvest or emigration. Nutrients tied up in organisms, plant or animal, are retrieved through decomposition, becoming available again for plant growth.

Most North American grasslands support aboveground consumer communities that are similar, consisting of large herbivores, invertebrates, small mammals, and birds. Consumer biomass structure is usually dominated by large herbivores (primarily domestic stock), with invertebrates second in biomass; rodents and birds make up only a small portion of the total primary consumer biomass (5). The following is a brief review of processes involving some of the important groups found in the California annual grassland ecosystem.

INVERTEBRATES

There are 4 classes of invertebrates normally represented in grasslands: Arachnida, Chilopoda, Deplopoda, and Insecta (19). In addition, the class Crustacea may represent a large percentage of the biomass in annual grassland because of the isopod _Armadillidum vulgare_. Most available information concerns insects, primarily grasshoppers.

The predominant grasshoppers in California annual grasslands are the devastating grasshopper (_Melanoplus devastator_), the clear-winged grasshopper (_Camnula pellucida_), the valley grasshopper (_Oedaleonatus enigma_), and _Dissosteira spurcata_, which has no common name (20). The devastating grasshopper is the most widespread and most numerous species; its nymphal stages feed on succulent legumes, filaree, and grasses. As plants on hills dry up in May and June, these grasshoppers migrate downhill, following succulent plants, and eventually may end up in swales where summer annuals grow or in croplands adjacent to the foothills. Thus, annual grasslands serve as a reservoir for grasshopper infestations. Temperature and rainfall play an important role in determining grasshopper populations (20). Grasshoppers also feed on dried grasses after vegetation dries up.

M. devastator is parasitized by the Dipteran Sarcophaga falciformis (Middlekauff, 1959). Adult female S. falciformis attack adult grasshoppers, injecting eggs into the grasshopper's body. Larva migrate to the thoracic cavity, and the grasshoppers usually die the sixth day after attack, when the mature maggot emerges (21). Middlekauff reported that this parasitism was primarily responsible for eliminating a population of 24 grasshoppers/m^2 over a two-month period. He reported that it was not difficult to find the hollowed-out bodies of grasshoppers killed by the maggots.

While little is known about the ecology of invertebrate herbivores, we know even less about invertebrate predators. Among these predators are centipedes, spiders, beetles, ants, and nematodes. One of the few studies dealing with this group was by Paris and Sikora (26), on isopods in California annual grasslands. They found that the ground cricket (Stenoplematus) preys on A. vulgare. Forty-eight per cent of the ground crickets they examined had consumed radio-tagged isopods. They also found some predation on isopods by lycosid spiders.

We know less about the structure and ecological function of the invertebrate fauna than of any other of the aboveground consumers in California annual rangeland. Invertebrates are difficult to study because of the diversification and specialization of life stages of various taxa, and because of the large number of taxa present. Yet, invertebrates probably comprise a greater portion of the aboveground biomass and have a greater influence on production than any other aboveground group.

HERPTILES

Most herptiles are carnivorous (12). Amphibians, such as the bullfrog (Rana catesbiana), feed primarily on insects (3); bullfrogs are subsequently fed on by garter snakes (Thamnophis elegans) (Fitch, 1949:565). The most abundant snake on California annual rangeland is the rattlesnake, estimated at 2.9/ha (Fitch, 1959:546), and the gopher snake, which Fitch (9) estimated to be approximately one-fourth as abundant as the rattlesnake. Both the rattlesnake and gopher snake feed primarily on rodents. Rodents composed 80% of rattlesnake diets and 70% of gopher snake diets (9). Although both snake species feed on the same prey species, there is a difference in the size of prey selected. The gopher snake is primarily a nest robber, feeding on unweaned young rodents and bird eggs, while the rattlesnake preys on larger animals that have already left the nest (9).

Lizards, such as the fence lizard (Sceloporus occidentalis), skinks (Eumeces gilberti), and alligator lizard (Gerrhinotus multicarinatus), feed on beetles, grasshoppers, leafhoppers, Jerusalem crickets, and isopods (17, 27). Alligator lizards also consume fence lizards and skinks (6).

BIRDS

The California quail (Lophortyx californicus) is abundant on the San Joaquin Experimental Range (22). This bird is a herbivore, feeding on plant seeds and sprouts. Young quail feed on insects (28). Horned owls (Bubo virginianus) and red-tailed hawks (Buteo jamaicensis) are very important rodent predators on annual rangeland (7, 11). Fitch estimated horned owl populations in the fall and winter to be between 14 and 25 individuals in an 810-ha study area (7); red-tailed hawks were estimated at one breeding pair per 130-ha on the San Joaquin Experimental Range in 1939 (11). Primary food sources for both species were rodents. The horned owl, being nocturnal, fed primarily on such nocturnal species as woodrats (Neotoma sp.), kangaroo rats (Dipodomys sp.), and picket gophers (Thomomys sp.). On the other hand, red-tails fed on diurnal species such as the California ground squirrel (Spermophilus beecheyi). Both birds fed on the cotton-tailed rabbit. Although Newman and Duncan (22) list 38 species of birds as permanent residents on the San Joaquin Experimental Range, we did not study birds because of their relative unimportance as primary consumers in grasslands.

SMALL MAMMALS

The California ground squirrel (Spermophilus beecheyi) has received attention because of its herbivorous habits and its potential for competition with livestock for herbage. The average population of ground squirrels, during the green forage season, consumes less than 1% of the aboveground standing crop biomass. Fitch and Bentley (10) stocked a 0.2-ha enclosure with 6 adult male ground squirrels, a number they considered to be 8 times the average concentration on surrounding rangeland. They considered the average adult density on rangeland, before birth of young, to be 3.7/ha. Grinnell and Dixon (14) arrived at a similar estimate. From their enclosure studies, Fitch and Bentley estimated that one adult ground squirrel eliminated, through all activities, 41 kg of forage during the green forage season. Using their estimate of 3.7 squirrels/ha, the total amount of green forage removed by ground squirrels would be approximately 153 kg/ha. Average yearly production on their study site (counting what squirrels destroyed) was 3,499 kg/ha in the squirrel enclosure (Fitch and Bentley, unpublished MS on file at SJER). Thus, squirrels destroyed 4% of the annual standing crop biomass at peak of production. Fitch (8) estimated that a California ground squirrel population of 3.7/ha would consume an average of 7.8 kg of green forage a month. Assuming the plants to be 75% moisture, this would be 2.0 kg dry weight, thus, consumption by ground squirrels would average 11.7 kg/ha during a 6-month growing season. Assuming an annual production of 3,499 kg/ha, consumption by ground squirrels would be 0.3% of production.

The pocket gopher (Thomomys bottae) may reach population levels of 44 breeding adults per ha (15), or a biomass of 0.36 g/m^2 (Table 1). Because rodent damage to rangelands is of some concern, we are conducting further studies of rodents in California's annual grassland system. A preliminary analysis of results indicates that, as consumers of primary production, rodents are no more important in the annual system than they are in other North American grassland systems.

DECOMPOSERS

The decomposer component of grasslands breaks down the primary production not consumed by herbivores, and eventually the herbivores themselves, into chemical elements which are returned to the soil and the atmosphere. As much as 75% of the energy captured annually by photosynthesis enters the decomposer food chain.

Dipterans and coleopterans feed on carrion; coleopterans and isopods feed on litter (Fig. 1). Litter is partially decomposed by earthworms, isopods, diplopods, dipterans, collembolens, and mites, while dead plant parts belowground are fed on by nematodes and earthworms.

The isopod Armadillidum vulgare consumes both green and dead vetch (Vicia sativa), thistle (Silybum marianum), and tarweed (Picris eihioides). A. vulgare apparently prefer green Silybum to dead; they feed on Vicia primarily after leaf-fall (24). When populations were high, Paris (25) found the average live weight biomass to be 9-14 g/m^2. Assuming a stocking rate of one 370-kg cow per 10 acres, cow biomass would equal only 5.18 g/m^2 (Table 1). The biomass of the California ground squirrel averages 0.2 g/m^2 (8).

The most important group involved in the turnover of energy trapped by photosynthesis is the microflora, composed of bacteria, actinomycetes, fungi, and algae. Bacteria alone are present in numbers of 2-9 billion cells/g of cultivated soil. Although not all bacteria are active at any one time, the liveweight biomass in the upper 15 cm of grassland soil may be as high as 4 kg/m^2 (2).

Although the soil ecosystem provides the basis for plant production, we know relatively little about it. The primary source of energy in the soil system is detritus (dead organic matter) provided by the death of plants and animals, or the egestion of animals (30).

Earthworms may contribute as much as one half of the total faunal biomass in the soil (1). Earthworms in the soil ingest 5-9 kg (dry weight) of soil/m^2 in one year (1). Small lumbricid and encyhytraeid worms, which live and feed within the surface litter, feed on dead plant fragments and their excrement consists chiefly of litter fragments (1). Thus, earthworms render dead plant material more susceptible to soil microorganisms. Although earthworms have some direct influence on litter decomposition, their greatest contribution to energy flow and nutrient cycling in the soil is their catalytic effect on litter decomposition (25). This effect results from stimulation of the growth of microorganisms, which account for most of the metabolic activity in the litter/soil complex (30). While soil invertebrate biomass may reach 220-240 g/m^2, the microflora biomass has been estimated at 1.6 kg/m^2 (1). Microorganisms may have positive influences on plant growth because microbial metabolites serve as major plant nutrients and microorganisms liberate nutrients from soil organic matter and minerals (13).

Ideally, we should use information on energy utilization by each component of a system to discuss energetic relationships, but this information is not available. Biomass is the best criterion we have available for inferring energetic relationships in ecosystems. I gathered the information in Table 1 from a wide assortment of publications and converted it to numbers per hectare and g/m^2 for comparison. While most of the information is from California annual rangeland, the original data were derived from studies conducted in different years at different locales. It is evident that there is a wide disparity in our knowledge of various groups of consumers. We can talk of biomass or numbers of specific species of rodents, birds, some herptiles, grasshoppers, and one decomposer, but we must lump all soil invertebrates into "Total Soil Invertebrates" and all microflora as "Total Soil Microflora." Yet, these two groups contain the greatest biomass and contribute the greatest part of total energy flow in the system. In addition to their contribution to total energy flow, these two groups are vital in nutrient cycles.

The importance of decomposers has been demonstrated by excluding them from containers of litter. In a nine-month study, 60% of oak leaf litter was left after exposure in containers that allowed access only to microorganisms and small invertebrates; in containers that allowed access to all decomposers, only 10% remained after nine months of exposure (4).

The mean daily rate for decomposition of leaf litter in a grassland system in New Zealand, 36-60 days after defoliation by livestock, was 18.9 kg dry matter per hectare per day (16). Decomposition rates were much lower immediately after defoliation but eventually reached nearly 35 kg/ha per day because of an increased leaf death rate. Thus, although decomposers utilize a very high percentage of the available energy produced by primary producers, decomposers are vital to the function of the grassland ecosystem. Without the decomposers, there would be buildup of litter and carrion, with a resulting accumulation of nutrients aboveground and an increase of trapped energy in the system. Nutrients would become tied up on the undecomposed material and would not be available for subsequent production, resulting in a decrease in primary and, eventually, secondary production.

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GROUP	FOOD	FUNCTION
EARTHWORMS	LITTER, MINERAL SOIL	COMMINUTION OF LITTER
		MIXING SOIL & LITTER
MOLLUSKS	LIVE & DEAD VEG.	PRIMARY DECOMPOSITION
ISOPODS	LITTER	COMMINUTION OF LITTER
DIPLOPODS	LITTER	COMMINUTION OF LITTER
		PRIMARY DECOMPOSITION
DIPTERANS	LITTER, CARRION	COMMINUTION OF LITTER
		PRIMARY DECOMPOSITION
CLEOPTERANS	DUNG, CARRION	PRIMARY DECOMPOSITION

Fig. 1. General composition, food sources, and function of grassland decomposers (adapted from Paris, 1969).

Table 1. Liveweight biomass of selected grassland consumers

Consumer	Relative density	#/Ha	g/m^2	Reference
Livestock	Light grazing	0.14	5.18	Wagnon et al. 1942
	Heavy grazing	0.28	10.36	
California ground squirrel	Average	3.70	0.21	Fitch 1948
Pocket gophers	High	44.00	0.36	Howard & Childs 1959
Red-tailed hawk	Average	0.02	-	Fitch et al. 1946
Rattlesnake	Average	3.00	-	Fitch 1949
Grasshoppers	?	240,000	-	Middlekauff 1959
Total soil invertebrates	?	-	220-240	Wiegert et al. 1970
<u>Armadillidum vulgare</u>	Low	-	0.17	Paris 1969
	High	-	14.00	
Total soil microflora	?	-	4,000	Clark 1969

CHAPTER VI

UTILIZATION PROBLEMS AND POTENTIAL OF THE CALIFORNIA ANNUAL GRASSLAND ECOSYSTEM

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Utilization, which I take to mean at least thoughtful management and, ideally, stewardship of the land, is potentially the most far-reaching and fundamentally important topic in the grassland ecosystem program. I had brief hopes of being able to distill the essence of some 50 years of research and thinking into 20 minutes or clear insight. I quickly concluded, however, that we must be content, for now, with a progress report on the compilation and integration of information related to utilization of the California (Mediterranean) annual grasslands (14).

For that work to go forward smoothly, efficiently, and effectively, this progress report will be widely disseminated to provide opportunity for constructive criticisms and useful contributions. Therefore, an outline of the Utilization section is presented with two objectives in mind: 1) to present my concept of what the Utilization section should include--this indicates my notions about its breadth and scope; and 2) to provide a basis for reaction and contribution.

OUTLINE OF UTILIZATION SECTION[2/]

1. The multiple-use concept (Introduction)
2. Agricultural crops vs. range and range pasture forage
3. Vegetation-type conversion
    - Objectives
    - Methods
        - Fire
        - Mechanical
        - Chemical
        - Biological
    - Major effects
        - Hydrologic
        - Watershed stability
        - Nutrient balance and cycling
        - Numbers and activities of wildlife and other populations
        - Cultural and ecomonic impacts
4. Revegetation
    - Life form
    - Soil
    - Species
        - Native
        - Resident (naturalized)
        - Introduced
    - Examination of the concept of a "weed"
    - Revegetation methods
5. Management, agricultural productivity considerations
    - A. Site selection
    - B. Plants
        - Fertilization
        - Symbiotic N fixation
        - Weed control
        - Pest control
        - Poisonous plants
        - Defoliation
            - Intensity
            - Frequency
            - Deferral
            - Residue left
        - Seed production (annuals)
        - Vegetation accumulation (perennials)
        - Fire
        - Aesthetic consideration
    - C. Soil
        - Geological-genesis
        - Hydrologic-watershed
        - Erosion-stability
        - Other edaphic
    - D. Animals
        - Species
            - Domesticated
            - Nondomesticated
        - Nature of product
            - Offspring
            - Growth (meat)
            - Other

2/Revised from the outline drafted by Robert G. Woodmansee for the proposed grassland-type synthesis volume entitled "Structure, Function and Utilization of the Annual Grassland Ecosystem"

D. Animals (CON'T.)
- Primary--secondary transfers ("harvesting")
  - Energy
  - Protein
  - Other
  - Efficiency
- Supplementation
  - Energy
  - Protein
  - Other
  - Efficiency
- Grazing systems
  - Objectives
  - Constraints
- Predation

E. Water
- Description of the resource
- Management opportunities related to agricultural productivity

F. Enterprise/industry structure
- Options in production systems
- Economic constraints

6. Management, public-domain considerations
   - Evolution of public and private control (historical)
   - Public vs. private decision and policy-making processes
   - Conflict and compatibility vis-a-vis agricultural use
7. Implications for the future
   - Role of research and teaching

Multiple-use concept

Let's start at the beginning, with the concept of multiple use. Meanings sometimes change over the years. One earlier interpretation of multiple use was that the land could be used for multiple purposes--livestock grazing, habitat for wildgame, recreation, and so on. That idea still remains and is valid, but a newer meaning derives from the knowledge that some resources are finite and nonrenewable and that what someone does in terms of use management in one location may very well have an influence, not always beneficial, elsewhere (29). It is the concept of planet earth, with limited resources. Dr. Simon Ramo, of TRW, Inc., which built the highly successful Pioneer satellites, said recently, "One of the first things we learned by going into space was that we were in space already. Man is an astronaut aboard a giant satellite called Earth..." We hear a lot about the problems of environmental pollution, and it is not an unfamiliar theme to rangeland managers. We also hear about the considerable opportunities for man's use of the 20-30 million acres of California annual range and wildlands. As someone has said, we do not have problems, only opportunities--we are faced with a number of insurmountable opportunities!

Agricultural crops vs. range and range pasture forage.

One topic may seem somewhat out of place here, but nevertheless may be important. That is, there is not an obvious categorical difference between the annual grassland ecosystem as identified in this symposium and agriculture as most of us think of it (30,39). In the earlier days of this state, before massive infusions of irrigation water, land-forming and drainage, there was much dryland farming, crops being grown with seasonal rainfall and whatever useful amounts of water could be stored in the soil profile. A little light should be going on about now, with the realization that the Mediterranean annual climate is the single common denominator for plant productivity patterns on our annual grasslands, dryland barley or alfalfa, and the clover fields promoted by Love (27,29,32) and later in Madera County by Emrick (16) and others. Thus, the geographical and utilization boundaries for annual range vary with the individual's point of view. Basically, there is little argument about the grazing of indigenous populations of grasses, legumes and forbs on unirrigated land. If water is added (or herbicides, or fertilizer, or introduced species), then what does it become (31)? And, geographically, at least in many parts of the annual system in California, true grasslands are commingled with small areas of land suitable for cropping or at least for supplemental irrigation of forages, forming a mosaic of use types, which interact to influence the utilization of each other. My point is not that we broaden the definition of range so greatly that it becomes unacceptable to those who have spent a lifetime of work with it, but, rather, to avoid the opposite extreme while at the same time recognizing that the utilization of grasslands may be quite different where there is a mosaic of vegetation types, cropping systems, and the availability of crop residues, not to mention water.

Vegetation-type conversion.

This section is divided into three subsections: Objectives, Methods, and Major effects. The original objectives, I believe, were quite straightforward--to make 2 blades of grass grow where one (or none!) grew before, by replacing shrubs and trees with open space for herbaceous vegetation, suitable for the desired domesticated livestock (37, 40). I am not at all certain whether the profound effect of type conversion on the hydrologic balance of the watersheds was anticipated, or was simply recognized when it subsequently occurred. Methods for achieving vegetation type conversion (VTC) involve the use of fire [control burns (15, 51) or wildfires (34, 35)], mechanical tools (6, 47), chemicals (23, 24) or biological agents (e.g., goats), singly or, more typically, in combination (37). Major effects of VTC are on hydrology (18, 54, 56), watershed stability (5, 10, 35), nutrient cycling and balance (25, 59), cultural (17) and economic (43, 44, 58) impacts, and populations of game, rodents, insects, birds, etc. (13). There is little doubt that relatively large-scale and uniformly applied VTC, as practiced in the 1950's and 60's, has diminished. There are reasons for this, including the simple fact that much or most of the land most suitable for such management has been converted. Legal restrictions on the use of fire (8), landowner liabilities, and the actual patterns of land ownership have almost eliminated its use by ranchers (33). The costs of mechanical clearing, and the costs and hazards of chemicals have greatly restricted their usage. To my knowledge biological means have been used mostly for follow-up control of resprouting woody plant species, and even that has been relatively minor, at least in California.

The major effects of VTC are important within the context of utilization and land stewardship. Hydrologic effects and watershed stability are not separable, independent items. The benefits of improved surface infiltration and deep percolation to subsurface aquafers which feed streams and springs are dependent on proper choice of site to begin with, the success of revegetation by herbaceous introduced and resident species, and management of these areas in succeeding years. When the geologic formations are not suitable, e.g., when subsurface slip planes permit movement during periods of heavy winter rainfall after the stabilizing element of roots of woody species has been lost (5, 10), and when slopes are too steep, or when the physical nature of the soils tends to make them susceptible to compaction and/or surface erosion, and when grazing management is not the best, the eventual outcome in terms of plant and animal productivity may be no more than the original condition, and can be even less. An issue which has emerged more recently, an issue of great contemporary importance, is the question of whether the final equilibrium status of essential plant nutrient cycling and balance in the soil system is more favorable, less favorable, or no different from what it was before. There are at least 3 considerations here, all are important to long-term utilization. One is the comparative physical and biological structure and function of a soil-plant system which consists substantially of deep-rooted woody species, whose canopy transpiration characteristics and nutrient pumping action maintain a certain kind of essential element distribution, vs. a soil-plant system based on shallow-rooted, seasonal, grasses, legumes, and forbs. A second consideration is the implied qualitative and quantitative changes often accompanying VTC where the attempt is made to introduce a sizeable proportion of legumes into the annual plant community (45). Soils of the California range are diverse and often intermingled (36). It is almost axiomatic that California range soils are poor in nitrogen, and also often poor in phosphorus and sulfur (45). In fact, one of the major arguments advanced in favor of legume introduction is that, once properly inoculated, nodulated, and established, they serve as a converter of atmospheric N_2 to plant protein, and therefore become a substitute for nitrogen fertilizer (39). It is also well known that the poor availability of soil P is, in many soils, substantially a function of inherent adsorption phenomena (1). Phosphorus fixation by soils is a worldwide problem, and the total chemistry of this element is very complex (2, 3, 21). You can see what I am leading to. Here is a combination of a physically disruptive action, namely conversion, followed by an attempt to introduce a new member into the changed plant community, a member whose growth requirements demand both that the nutrient status and balance of the soil be substantially changed, and, more important, that that change be maintained from that point forward. To say that problems are involved is probably an understatement. A third consideration follows quite naturally from the underlying objective of VTC. Unless this parade of management activities and resource inputs is followed by heavier stocking pressures and increased levels of animal product yield sufficient to recover the various costs in a reasonable length of time, the work will have been largely for naught. Heavier stocking pressures mean more animal traffic and opportunities for soil compaction, and the cutting effect that Australians refer to as "pugging." Assuming that we are not talking about a closed ecosystem, but rather one from which there are significant levels of EXPORT animal product, there will be both a removal from the system as animals leave, and there will be redistribution within the system, through selective grazing and patterns of animal waste distribution. Now, admittedly, the things I am talking about may be quantitatively "small" and difficult to deal with on an annual basis. On a long-term basis, however, in terms of generations or, at very least, decades, they are significant, and this is one of the major points I wish to make--that UTILIZATION be thought of in terms of long-range stability and maintenance of a reasonably balanced ecosystem, aside from the year-to-year cash flow, domestic livestock "cropping," and the amenity values of other use benefits. It may be maintenance of what is there now, unmanipulated, or it may be maintenance of some "improved" state.

I do not wish to minimize the importance of cultural and economic impacts and the effects of VTC on wildlife by touching this topic lightly. These two together, in fact, could very well serve alone as the basis for a full 20-minute presentation. This is the day of Environmental Impact Reports and Draft Environmental Impact Statements (48). It is also, perhaps unfortunately, the day of the acronym. We've added quite a few since the CCC and the Triple A. We have all heard about NEPA (the National Environmental Policy Act, or Public Law 91-190, passed in 1970), and we have heard about CEQA (the California Environmental Quality Act, passed in 1971). We are familiar with OSHA and Cal-OSHA. We have watched, almost in awe, as the grand scenario of Tahoe Basin unfolds, and a few may recall, as an example closer to the subject at hand, an article in the Sierra Club Bulletin entitled The Rape of the Elfin Forest. We will see more of this before we see less (12, 19, 42) and the outcome may have profound effects on structuring the permissible uses of land.

Revegetation

I've set revegetation apart as a major topic rather than as a subsection of Vegetation-type Conversion because in many cases only a managed shift in botanical composition of an already herbaceous plant community is involved (16, 29, 39, 60). Within this Revegetation section we need at least to think about life-form (i.e., perennials, annuals, herbaceous and woody), and species (native, resident, and introduced), the concept and significance of that unfortunate noun a "weed" (28, 49, 52), and, finally, revegetation methods (6, 20, 22, 23, 37, 40, 45). Lively discussions can arise around the statement: "Perennial grasses were once the dominant life form in California grasslands" (4, 9). The record, I believe, is too scanty to prove the issue one way or the other beyond a reasonable doubt. My only comment at this point is that for an area as large as the state of California, with as much diversity as it has in landforms, soils, and climate, it seems unlikely that the original vegetation was very uniform. What is more disturbing is that the present-day complex of annual vegetation and Mediterranean climate is not well understood outside the boundaries of our state (if even within it!), and I have seen it referred to as the Pacific Bunchgrass Region in a textbook published as recently as 1973.

We have introduced perennials, for various reasons, including the expectation that they would significantly extend the season of plant production and increase the total yield of dry matter (20, 22, 26, 38, 40, 60). We have introduced annuals, especially those of the genera Trifolium and Medicago, the clovers and medics (20, 39, 44), and I think it is fair to say that overall we have been more successful with the annuals than with the perennials. Perhaps the classic example is Trifolium hirtum, "rose clover" (39). The value of rose clover as an addition to our grasslands flora is unquestioned. What is a little more tricky is when does an annual plant become that nefarious blackguard called a "weed" (28). It is interesting to me that the Australian views on what are weeds and what are acceptable range forage plants is sometimes different from ours. A chap whose opinions on various and sundry issues I respect very highly, said to me a few years ago, "You know, there is more beef produced on Bromus rigidus in California than most people are willing to give credit for." Eventually, it appears, this sort of thing really boils down to a relative assessment of undesirable characteristics of the prominent herbaceous species available for grazing, including their injurious properties and their poor yielding ability. Even as desirable a plant as subclover is not immune from criticism--for example, its estrogenic compounds (50) and rapid leaf shatter on reaching maturity. The other interesting element is: when does one call a retreat from battle with an undesirable invader. Medusahead is a good example (61), and I have heard it said that it should be considered as a bona fide resident species and be done with it, particularly when the costs and restrictions on use of chemicals are taken into account.

I'd like to spend a few moments on Revegetation Methods, because it provides an opportunity to introduce a couple of ideas important in utilization related to plant introduction. One is the complex nature of the establishment phase of revegetation (36), the other is the importance of colonizing ability.

I believe I have coined two additional words for the ANNUAL grasslands literature, namely, "micro-establishment" and "macro-establishment." Micro-establishment" is the initial, single-plant establishment sequence, which begins with sufficient fall rain, or with adequate seed inhibition when a seeding is made subsequent to adequate fall rains [an example of the latter would be the range drill-contact herbicide technique developed by B. L. Kay (22)]. The introduced seeds germinate, and seedlings become established and complete their phenological life cycle, including mature seed set. "Macro-establishment" involves, in this context, stand establishment, over a minimum of 5 years following the original introduction. In almost every instance, physical spread of vegetative cover beyond that resulting from successful "micro-establishment" is required, together with a concomitant process of seed reserve multiplication (46). In short, "macro-establishment" means that the newly introduced plant species or cultivar has become an accepted and stable member of the plant community, which itself has been managed in a definable way.

If one ponders these biological realities in relation to the additional general requirements of dollars for seeds, pelleting, fertilizer, seeding, possible fencing for needed control of grazing, and ongoing management (labor), one must conclude that much care is required in choosing among range-improvement alternatives. I believe that one cannot overemphasize the long-term importance of plant species, especially legumes, which combine a high level of tolerance to the vicissitudes of the grassland environment with strong colonizing ability. Neither of these is adequately understood, and especially the latter. Possibly this is because we have tended to overemphasize short-term responses to manipulation of competition, fertility, and grazing management and have not balanced these necessary investigations with corollary investigations of population dynamics as seen from the viewpoint of plant breeding systems, and with long-term studies of the various strategies and tactics which make a species a good colonizer.

Management

The remainder of the outline, which consists essentially of "Management" as seen from two broadly different points of view, and some "crystal-balling" of the future, is mostly a refinement and reinterpretation of the preceding topics. The remainder of this "progress report" touches only lightly on but a few of the topics and subtopics.

Implicit in the concepts of "utilization" and "management" of any complex land system is the notion of Site Selection. Probably a major weakness in the interpretation and dissemination of research results has been the tendency to extrapolate and generalize too liberally from the data and conclusions obtained from small plots. Planning, execution, and interpretation of research have been heavily influenced by the two basic elements of experimental design and statistical analysis, the measure of central tendency and the measure of dispersion, both often applied with the assumption that randomly distributed populations are involved. In this regard, the availability of high-speed computers and sophisticated software, plus indications of new patterns of thought about application of the "scientific method" (e.g., 41) provide great promise of providing the means for conduct of multidisciplinary research in a manner more nearly like the actual workings of the grassland ecosystem, combining the intricacies of site mosaics with asymetrical utilization patterns over time.

Returning to "Site Selection," it is important that some standardized system of site classification be provided. An excellent beginning has been provided in several publications out of the San Joaquin Experimental Range (e.g., 7, 57).

I offer below an analog approach, intended to provoke reaction leading to constructive criticism and sound suggestions for its improvement.

ANNUAL GRASSLAND SITE CATEGORIES

I. Range-brush-woodland, with numerous climatic, physiographic, and edaphic limitations, not ordinarily amenable to physical manipulation, suitable only for extensive[1/] management.

II. Dryland, with essentially complete herbaceous vegetation, with minor climatic, physiographic, and edaphic limitations, arable and fenced, suitable for intensive[2/] and uniform management.

III. Mosaic of site types, with corresponding limitations to uniform intensive management, but suitable either for "mosaic" approach to management or for extensive management.

1/ extensive management: mechanical manipulations largely limited to clearing and sprout control; reseeding/revegetation opportunities largely limited to the time immediately following clearing (e.g., seeding into "white ash spots," assuming sufficient dry fuel load); principal on-going management options largely limited to aerial application of fertilizer, grazing management related to type and number of animals and season of use; animals may be thought of as a "biological tool" in resource management, e.g., as desseminators of plant species of high colonizing ability, and for their roles in nutrient cycling and plant species manipulation through time-specific grazing pressure.

2/ intensive management: tillage, seedbed preparation, and mechanical seeding/fertilizing operations possible on at least three-quarters of a defined land area unit, using medium- or small-scale agricultural machinery; supplemental irrigation often possible; fencing permits a high degree of control over season of use and grazing pressure; trophic-level transfer can be highly efficient, and the principal role of the animal is as a harvester and efficient converter of plant productivity; land areas may be rotated in a dryland cropping system.

These three categories certainly represent a gross oversimplification, and they are intended primarily as a point of departure. I hope, however, that the final draft of the grassland ecosystem volume will contain a realistic, functional scheme, useful for descriptive, management, and research purposes. I earnestly invite suggestions, to this as well as to any other segment of the Utilization outline.

The remainder of the "management, agricultural productivity" will be left to the next approximation of this "working draft," pending the expected and considerable assistance of W. J. Clawson, B. L. Kay, R. M. Love, J. E. Street, and D. T. Torell, as well (I hope) of many others who are intrigued by the potential for putting together, in one place, a true "state of the art" compilation about what is known (and not known) about the workings of the annual grasslands. In this regard, we have an excellent beginning, as the aggregation of papers in this Anaheim Symposium demonstrates. We need to put together a NASA-type effort, but it won't cost nearly as much if we take advantage of our opportunities to work together and if we communicate effectively.

IMPLICATIONS FOR THE FUTURE

Finally, a bit of conjecture and speculation about Implications for the future. Progress in understanding and utilization of the annual range grasslands and wildlands will come about as we are able to do the following:

I. Improve our ability to understand the system as a whole, over useful lengths of time. Especially important are the interactions among vegetation, soil, and watershed management related to climate, nutrient balance, availability and cycling, and vegetative phenology and population dynamics.

II. Improve our use of renewable and nonrenewable resources in the grazing food chain, while at the same time maintaining good stewardship of the land. One definition which has been advanced is to "balance development with preservation; this equals conservation." Three elements are of importance. One is efficient and effective trophic-level transfer, with emphasis on the proper role of the remarkable ruminant. Another is effective use of water, whether as precipitation or supplemental irrigation; it is a resource input of crucial importance and any deliberate management must be concerned with water quality. The third is effective use of soil nutrients, with emphasis on nitrogen, and the elements related to legumes and symbiotic nitrogen fixation.

III. Accelerate the trend toward a mosaic approach to management. This is simply bringing the concept of "multiple use" up to date. We will manage some rangeland more intensively, i.e., in a manner closer to Valley agriculture, and we will manage some more extensively, and within a longer time-frame. It is here where the power of the computer can be brought to bear most effectively, assuming the development, based in many specific instances on new research, of an adequate sitepotential management-opportunity matrix.

IV. Resolve the "Ultimate Irony" of Economics and Efficiency. Much will be made of dollar economics vs. energy economics (and if energy, which kind--caloric or fossil fuel?). Efficiency is a slippery concept (55), and the simple equation $E = P/R$ can provide almost any desired answer, depending on the assumptions and units of P and R. The prestigious Cervinka-Chancellor report on energy use in California agriculture (11) showed that only about 5% of the total energy used in California on an annual basis could be assigned to production agriculture. Grasslands agriculture, of course, would consume only a small fraction of that 5%. Two per cent each of the nitrogen and phosphorus fertilizer used in California is accounted for by range.

The combination of large nonagricultural land areas, largely untended vegetation, the natural hydrologic cycle, and the ruminant animal provide in this context a remarkable opportunity for augmenting the nation's food basket while at the same time carrying on the serious responsibility of stewardship of the land (34).

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CHAPTER VII

SIMULATION MODELING OF THE ANNUAL GRASSLAND ECOSYSTEMS

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Annual grassland ecosystems, like all farming systems, are essentially biological systems that are managed for economic gain. An important feature of annual grassland, however, is that animals consume it to obtain all or most of their nutritional needs. Thus, the producers and consumers are combined in situ, resulting in great complexity of organization; and our knowledge of the components and their interactions is very incomplete. Moreover, our efforts have been fragmented into specialized areas of research, which has resulted in communications problems among researchers. Thus, an integrated approach is required, and modeling is a way of achieving such integration.

Secondly, grazing experiments are extremely costly per unit of information obtained, and computer simulation (or modeling) is a way of maximizing the use of the data that we do have, in addition to pointing to critical areas of needed research. Thus, it can be an aid in establishing research priorities.

Three modeling areas are referred to next to illustrate some of the potentials: 1) annual grassland ecosystem; 2) a management-oriented simulation model of deferred grazing of subclover by sheep; and 3) operations research techniques.

ANNUAL GRASSLAND ECOSYSTEM MODEL

We plan to adapt ELM, the grassland ecosystem model developed at the Natural Resources Ecology Laboratory, Colorado State University, to the annual grassland during the next year (Fig. 1). Since this lies in the future, a preview will be attempted, touching on the highlights of the present ELM model as adapted to the shortgrass prairie type (Woodmansee and Hunt, 1975).

ELM is a dynamic simulation model that solves first-order difference equations using a daily time step. It is coded in SIMCOMP, a FORTRAN-like simulation language developed at the Laboratory. It is concerned primarily with biomass and energy considerations as influenced by the abiotic, producer, consumer, and decomposer components of the ecosystem, though water and nutrients are also included. Either historical or simulated weather data may be used as driving variables, and temperatures of both soil and air receive attention. Submodels include: plant biomass in five species groups, plant phenology (temperature driven), water, mammalian consumer (8 species), insect consumer, decomposer, nitrogen, and phosphorus submodels.

A number of specific questions have been addressed in the development, testing, and operation of the model, with the following results:

1) What is the effect on net or gross primary production as the result of the following perturbations:

   a) variations in the level and type of grazing,
   b) variations in the precipitation or applied water or air temperatures, and
   c) variations in added nitrogen or phosphorus?

Results of simulated perturbations in items (a) and (b) have generally been satisfactory. Results for fertilizer treatments (c) have been unsatisfactory so far.

2) How is the carrying capacity (i.e., maximum sustainable domestic herbivore stocking density) of a grassland affected by these perturbations? In most cases responses of the model to this type of question have been satisfactory.

3) Are the results of the model run consistent with field data taken in the Grassland Biome program? This question is asked of each model run, so the examples are countless. The answer to this question is yes and no and maybe.

4) What are the changes in botanical composition as a result of these perturbations?

We can track the relative changes in the biomass of five primary producer groups (warm- and cool-season grasses, forbs, shrubs, and cacti). Runs have been made simulating up to 5 years of system response.

The model is a research tool to use on a par and in conjunction with field, laboratory, and literature studies. Through exercising the model and attempting to follow the dynamics of aboveground plant material, attention has been focused on the importance of the process of the fall of standing dead material to litter. Our ignorance of that process was clearly indicated. This flow has been isolated as a key process in grassland ecosystems. Results of the experiments will refine and better quantify the current representation of the process in the model.

ELM is a vehicle which can be used to study the interactions of difficult-to-study parts of the ecosystem, e.g., the belowground system. To study the interactions within the system, definition of the belowground system was essential. The model has been used to gain insight into such processes as root death, microbial activity and inactivity, the role of microorganisms in nutrient cycling, and root respiration, to mention only a few.

The goals of the ecosystem modeling effort were to create a model that would serve as a communications device and organizer of information which would be useful as a research tool and would yield results that could help elucidate biological phenomena in grassland ecosystems. The objectives obviously place some rigid constraints on the model usability, but if those constraints are satisfied, then the model, if appropriate questions are asked and the answers are adequately interpreted, can aid biological understanding, attain the stated goals of modeling, and suggest management implications.

SUBCLOVER, DEFERRED-GRAZING MODEL

This model is focused on answering a specific management question: under what conditions is deferred grazing of seedling subclover a profitable management tool? The model concerns winter production of an annual-type legume-dominated forage resource and the weight gains of sheep grazing it (Smith and Williams, 1973). These processes depend on interactions among pasture plants, climate, soil, and animals. It is beyond the scope of any single grazing experiment to control and vary individually all these factors. However, processes that determine the liveweight response of sheep grazing a Mediterranean annual type of pasture are sufficiently well understood to attempt an integrating model.

The model relates particularly to a grazing experiment, conducted by Dr. R. C. G. Smith in W. Australia as part of his Ph.D. research, combined with data from the literature. The main experiment consisted of 8 paddocks (0.4 ha each) of Woogenellup subclover sown on virgin land so that virtually pure clover resulted. Four of the paddocks were grazed continuously from emergence, and four were deferred for 5 weeks. Detailed plant and animal measurements were taken over the 105-day growing season.

Central to the model is the transformation of energy and matter to sheep liveweight (Fig. 2). The differential equations to calculate the rate of conversion involve consideration of the growth rate of pasture, its rate of removal by grazing, and the conversion of ingested pasture to sheep liveweight. For the solution of these equations, other functions are used to calculate the weight of herbage produced, pasture height, plant density, herbage intake and digestibility, soil moisture, and other phenomena. The model was written for computer simulation in Fortran, and the equations are solved numerically by use of difference equations.

Autumn deferment is a method of grazing management associated with the Mediterranean annual pasture in which animals are removed from pasture after the opening rains and are fed from alternate sources while the pasture reestablishes. A response to deferred grazing has been postulated on the basis of increased leaf area and light interception during early growth. Factors known to affect the response to deferred grazing are: 1) stocking rate; and 2) pasture species. Two factors not examined so far in experiments but which might be anticipated to have a major bearing on both the response and cost of deferred grazing are the length of deferment and initial plant density. The main objective of this study was to postulate by computer simulation the probable importance of these two factors in relation to stocking rate (Smith and Williams, 1974).

To examine the potential utility of a dynamic model of early pasture growth and animal production for optimization in deferred grazing, economic weights were given to the predicted output of liveweight and input of oats for a range of grazing strategies. In the production system simulated the following assumptions were made:

a) Sheep were fed a maintenance ration of oats (Digestibility = 0.72) while deferred.
b) Under grazing, sheep were fed a maintenance ration of oats when daily liveweight loss exceeded 0.3% of their liveweight.
c) Initial liveweight of sheep at emergence was 27.5 kg.

The model predicted that total liveweight change per hectare is markedly dependent on both stocking rate and length of deferment. The response to length of deferment becomes more marked with increasing stocking rate, and the response to both factors increased at higher plant densities. The model also indicated that optimal combinations of stocking rate and length of deferment at the one site could vary widely with variations in initial plant density and economic weights given to the supplementary feed input and animal output (Table 1). Therefore, in the practical situation an optimal combination will need to be estimated for each site and system of production. It is in this context that a dynamic model may well be a useful, and perhaps indispensable, aid to the decision-making process.

The performance of the model was stable and in accord with our understanding of the system. This stability can be attributed to negative-feedback loops in the model which tend to reestablish an equilibrium. Both stocking rate and length of deferment appear to interact to determine the response to deferred grazing. Therefore, to maximize the return from deferred grazing these two factors would need to be considered together. That has not yet been done in actual grazing experiments.

Table 1. Approximate combinations of stocking rate and lengths of deferment to maximize gross margin at different initial plant densities and liveweight values.

Plant density pl dm^{-2}	Gross margin \$ ha^{-1}	Stocking rate sheep ha^{-1}	Length of deferment days
	Liveweight \$.05 kg^{-1}		
10	.68	5	8
20	1.58	8	9
40	2.61	13	23
	Liveweight \$.10 kg^{-1}		
10	3.30	11	42
20	7.07	18	42
40	11.70	24	40
	Liveweight \$.20 kg^{-1}		
10	19.98	28	62
20	30.43	31	56
40	40.79	36	52

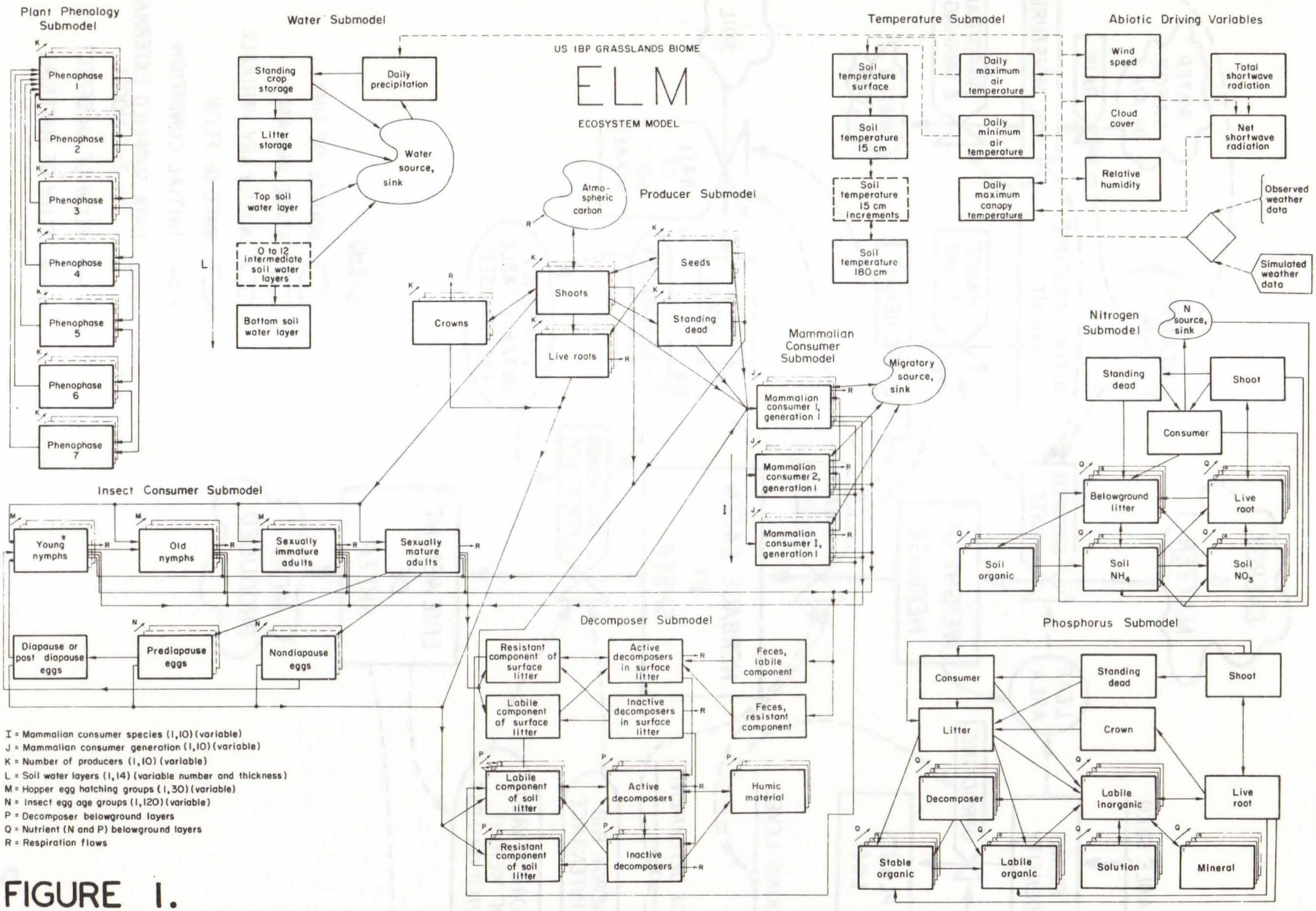
US IBP GRASSLANDS BIOME
ELM
ECOSYSTEM MODEL
Plant Phenology Submodel
Phenophase 1
Phenophase 2
Phenophase 3
Phenophase 4
Phenophase 5
Phenophase 6
Phenophase 7
Water Submodel
Standing crop storage
Daily precipitation
Litter storage
Water source, sink
Top soil water layer
0 to 12 intermediate soil water layers
Bottom soil water layer
L
Temperature Submodel
Soil temperature surface
Soil temperature 15 cm
Soil temperature 15 cm increments
Soil temperature 180 cm
Daily maximum air temperature
Daily minimum air temperature
Daily maximum canopy temperature
Abiotic Driving Variables
Wind speed
Cloud cover
Relative humidity
Total shortwave radiation
Net shortwave radiation
Observed weather data
Simulated weather data
Producer Submodel
Atmo-spheric carbon
Seeds
Shoots
Standing dead
Crowns
Live roots
Mammalian Consumer Submodel
Migratory source, sink
Mammalian consumer 1, generation 1
Mammalian consumer 2, generation 1
Mammalian consumer I, generation I
Insect Consumer Submodel
Young nymphs
Old nymphs
Sexually immature adults
Sexually mature adults
Diapause or post diapause eggs
Prediapause eggs
Nondiapause eggs
Decomposer Submodel
Resistant component of surface litter
Active decomposers in surface litter
Feces, labile component
Labile component of surface litter
Inactive decomposers in surface litter
Feces, resistant component
Labile component of soil litter
Active decomposers
Humic material
Resistant component of soil litter
Inactive decomposers
Nitrogen Submodel
N source, sink
Standing dead
Shoot
Consumer
Belowground litter
Live root
Soil organic
Soil NH₄
Soil NO₃
Phosphorus Submodel
Consumer
Standing dead
Shoot
Litter
Crown
Decomposer
Labile inorganic
Live root
Stable organic
Labile organic
Solution
Mineral
I = Mammalian consumer species (1,10) (variable)
J = Mammalian consumer generation (1,10) (variable)
K = Number of producers (1,10) (variable)
L = Soil water layers (1,14) (variable number and thickness)
M = Hopper egg hatching groups (1,30) (variable)
N = Insect egg age groups (1,120) (variable)
P = Decomposer belowground layers
Q = Nutrient (N and P) belowground layers
R = Respiration flows

FIGURE 1.

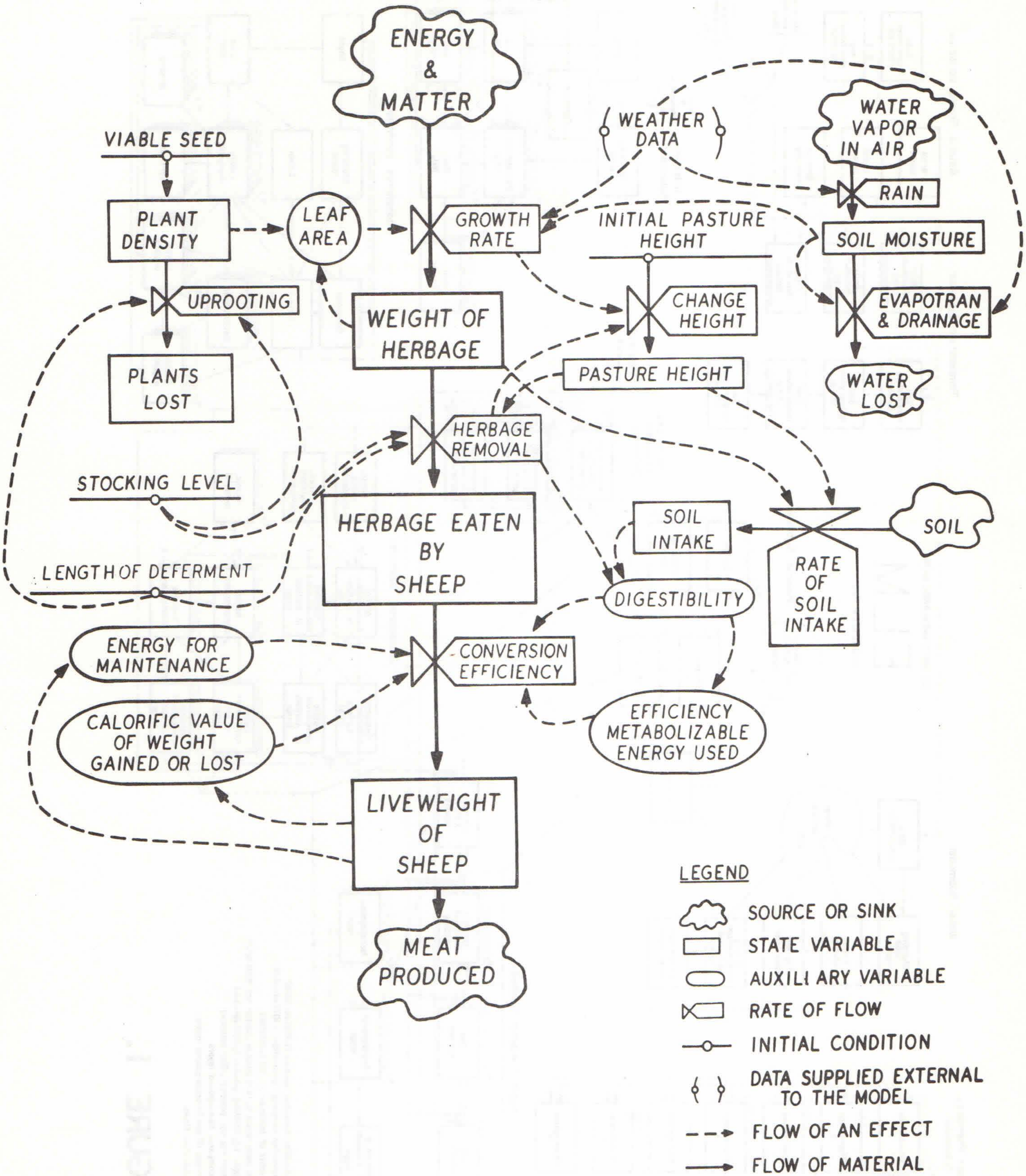
ENERGY & MATTER
VIABLE SEED
WEATHER DATA
WATER VAPOR IN AIR
PLANT DENSITY
LEAF AREA
GROWTH RATE
RAIN
INITIAL PASTURE HEIGHT
SOIL MOISTURE
UPROOTING
WEIGHT OF HERBAGE
CHANGE HEIGHT
EVAPOTRAN & DRAINAGE
PLANTS LOST
PASTURE HEIGHT
WATER LOST
HERBAGE REMOVAL
STOCKING LEVEL
HERBAGE EATEN BY SHEEP
SOIL INTAKE
SOIL
RATE OF SOIL INTAKE
LENGTH OF DEFERMENT
DIGESTIBILITY
ENERGY FOR MAINTENANCE
CONVERSION EFFICIENCY
CALORIFIC VALUE OF WEIGHT GAINED OR LOST
EFFICIENCY METABOLIZABLE ENERGY USED
LIVEWEIGHT OF SHEEP
MEAT PRODUCED
LEGEND
SOURCE OR SINK
STATE VARIABLE
AUXILIARY VARIABLE
RATE OF FLOW
INITIAL CONDITION
DATA SUPPLIED EXTERNAL TO THE MODEL
FLOW OF AN EFFECT
FLOW OF MATERIAL

FIGURE 2.

OPERATIONS RESEARCH TECHNIQUES

Operations research techniques are designed to optimize resource allocation. They have been used for military, industrial, and business management since the 1940's but only recently applied to range management problems (Jameson et al., 1974). Linear programming, a basic tool of operations research, has been used by John Menke, Forestry, U.C., Berkeley, to develop a management plan for grazing operations at the Hopland Field Station (Menke, 1975).

The fundamental idea is to solve a set of equations which are based on alternative assumptions about the allocation of resource components. The goal is either to maximize profit or to minimize costs. Also included are equations that reflect physical or economic limitations on use of the resource components. The solution of such equation sets is usually complex enough to require a computer, but computer speeds allow one to consider numerous alternatives in the management scheme and calculate the degree of sensitivity to changes in resource components. Results from the linear-programming approach and some of the other sophisticated techniques of operations research show much promise of aiding in ranch management decisions in a fast-changing economic climate.

SUMMARY

Several mathematical modeling techniques have been mentioned briefly. These techniques, when properly utilized, can be powerful aids to acquiring a better understanding of the complexities of the annual grassland ecosystem. We hope that through improvement of existing models and development of appropriate new models, we will be able to continue to increase our understanding of biological and management phenomena.

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